

---

Volume 86  
Number 3  
1999

Annals  
of the  
Missouri  
Botanical  
Garden



---

REVISION OF  
*BEILSCHMIEDIA*  
(LAURACEAE) IN THE  
NEOTROPICS<sup>1</sup>

*Sachiko Nishida*<sup>2</sup>

---

ABSTRACT

The neotropical species of *Beilschmiedia* are revised here, including general descriptions for morphology, anatomy, biogeographic distribution, and seed dispersal. The systematic position of *Beilschmiedia* within the family, as well as the systematic treatment of its neotropical species, is provided. As a result, 28 species were recognized with 4 newly described and 2 newly combined; they divide into five species groupings based on their leaf anatomical characters.

---

Lauraceae contain many taxa that are important ecological and economical components of tropical forests. However, the taxonomy of the family has not been sufficiently clarified at either the genus or species level. *Beilschmiedia* is an example of such a poorly understood genus.

*Beilschmiedia* is one of the largest pantropical genera in the Lauraceae, comprising about 250 species. It is usually distinguished from other laurel genera by the following characters: bisexual and trimerous flowers, six equal to subequal tepals, six to nine fertile stamens with 2-celled anthers, sta-

minal glands only in the third whorl, shallow receptacles, and fruit lacking cupules.

This genus is still poorly understood taxonomically. Since Meisner (1864) revised *Beilschmiedia* with the rest of the family, no revision for the entire genus has been written. For neotropical species, Kostermans's (1938) work was the most recent comprehensive revision, and Allen (1945) treated the Mexican and Central American species. These two revisional works were not based on abundant material; 7 of 15 species in Kostermans's revision and 4 of 8 species in Allen's revision were known only

---

<sup>1</sup> This study, undertaken as part of the author's doctoral dissertation research at Kyoto University, Japan, was mainly done during a stay at the Missouri Botanical Garden. I thank Hiroshi Tobe for his encouragement, Henk van der Werff for his guidance, and all the Garden staff for their support during my stay. I also thank the curators of the following herbaria: A, B, BM, BR, C, CR, F, IEB, INB, K, LL, MEXU, NY, P, R, RB, S, U, US, and VEN. I am especially grateful to the curators of MO, NY, and RB for allowing me to remove leaves from their specimens for leaf anatomy studies. Barry Hammel, William Haber, and the INB staff, especially Renaldo Aguilar, assisted me during my fieldwork in Costa Rica. J. L. Clark and K. Thomsen kindly sent me slides or materials of *Beilschmiedia*. Roy E. Gereau, as well as Hidetoshi Nagamasu, improved the Latin diagnoses. John Myers drew the fine illustrations. This research was supported by the Grant-in-Aid for JSPS fellowships from the Japanese Ministry of Education, Science, Sports and Culture.

<sup>2</sup> Division of Phylogenetics, Museum of Nature and Human Activities, Hyogo, Yayoigaoka 6, Sanda, 669-1546, Japan.



from the type collections. Additionally, 15 new species have been described under *Beilschmiedia* in the Neotropics since Kostermans's revision.

Collections of neotropical *Beilschmiedia* have increased to more than eight times as many as examined by Kostermans (1938). This present revision recognizes 28 species within *Beilschmiedia*, including 4 that are new to science.

#### MATERIALS AND METHODS

Approximately 850 collections from A, B, BM, BR, C, F, FCME, IEB, INB, K, LL, MEXU, MO, NY, P, R, RB, S, U, US, and VEN were examined. Fieldwork was carried out in Costa Rica in March 1996 to observe the habits and habitats for several species and to collect material for anatomical study.

#### TAXONOMIC HISTORY

The genus *Beilschmiedia* was first described by Nees (1831) with two Asian species, *B. roxburghiana* and *B. fagifolia*. For the Neotropics, many species now classified in *Beilschmiedia* were first described under *Hufelandia*. Nees (1833) described *Hufelandia* with *H. pendula* and *H. thomaea*, and since then 12 neotropical species were described for *Hufelandia*. Hemsley (1882) transferred the generic type of *Hufelandia* to *Beilschmiedia*, but Mez (1889) subsequently restored *Hufelandia* to generic rank. Kostermans (1938) later submerged *Hufelandia* within *Beilschmiedia* again.

Synonymous with *Beilschmiedia* in the Neotropics is *Bellota* Gay. Gay (1849–1852) described *Bellota* with a Chilean species, *B. miersii*, but Kostermans (1938) submerged this species in *Beilschmiedia*. Kostermans (1938) listed three other synonyms in his revision: *Boldu* Nees (non Feuillée), *Boldus* Kuntze (non Adanson), and *Wimmeria* Nees ex Meisner. However, *Boldu* Nees is a superfluous name. *Boldus* is a name that Kuntze (1891) reestablished from *Boldus* Molina, which actually belongs to the Monimiaceae. *Wimmeria* refers to a specimen label name for *Beilschmiedia pendula* and is not validly published. Kostermans (1952) combined the neotropical genus *Anaueria* with *Beilschmiedia*. However, Richter (1981) found that *Anaueria* differs from *Beilschmiedia* in wood anatomy. This, combined with differences in flower and fruit morphology, resulted in the current recognition of *Anaueria* as a distinct genus.

#### MORPHOLOGY AND TAXONOMIC CHARACTERS

*Habit.* All neotropical *Beilschmiedia* species are trees, with many of them growing about 30 m tall, occasionally up to 40 m tall.

*Leaves.* Species display two patterns of phyllotaxis, one with alternate leaves and the other with opposite leaves (for the species corresponding to each phyllotaxis, see Table 1). Species with alternate leaves rarely show a subopposite leaf arrangement near the tip of the twigs. Some species such as *Beilschmiedia anay* and *B. manantlanensis* tend to have leaves crowded at branch apices.

Leaf shape ranges from ovate to obovate. Size and shape of the leaves vary within many species. Leaves of *Beilschmiedia costaricensis* and *B. tovarensis* are especially variable.

Glaucousness on lower leaf surfaces is usually consistent within a species, but sometimes exceptions occur. A few collections of *B. mexicana* and *B. riparia* have glaucous leaves, although typical collections of these two species do not. In many southeastern Brazilian species, the presence or absence of a glaucous bloom is unknown because all the collections examined were supposedly placed in alcohol.

There has been no *Beilschmiedia* species reported to have domatia, but a few collections of *B. riparia* (Lorea 5498, Maya 1296, L. C. Rodríguez 374, and Wendt & Rico 4338) that have tufts of hairs in the axils of secondary veins appear to have domatia.

*Venation patterns.* Terms used here are sensu Hickey (1973, 1979), Christophel and Rowett (1996), or Nishida and Christophel (1999). Venation patterns of neotropical *Beilschmiedia* species were described in detail by Nishida and Christophel (1999). All neotropical *Beilschmiedia* species have penninerved leaves. Tertiaries of *B. alloiophylla*, *B. anay*, *B. latifolia*, *B. ovalioides*, *B. riparia*, and *B. tilaranensis* are usually strongly percurrent (directly connected to adjacent secondaries); those of *B. costaricensis*, *B. hexanthera*, *B. immersinervis*, *B. ovalis*, *B. steyermarkii*, and *B. tovarensis* are often weakly percurrent. The minor venation pattern (pattern of higher-order veins) can be used to delimit neotropical *Beilschmiedia* species. According to Nishida and Christophel (1999), the species roughly divide into two groups according to their minor venation pattern being fine or coarse. In species with a fine venation pattern, the highest vein order is seventh or more, and areoles (the smallest areas of the leaf tissue surrounded by veins) are usually less than 0.5(–0.7) mm diam. (Fig. 1A, B). In a coarse venation pattern, the highest vein order is less than fifth with larger areoles over 1.5 mm diam. (Fig. 1C). For species corresponding to each pattern, see Table 1. The veinlet pattern within areoles ranges from none (without a free-ending veinlet inside as in Fig. 1A) to branched



Table 1. Species groupings within neotropical *Beilschmiedia* based upon morphological and anatomical characters. Species with asterisks (\*) were not examined for leaf anatomy.

	Phyllotaxis	Minor venation pattern	Cuticular characters	Vascular bundle arrangement in midrib	Species name	Rough geographical distribution
<i>B. costaricensis</i> group	alternate	fine	<i>B. costaricensis</i> type	ring	<i>B. alloiophylla</i>	Central America, Andes
					<i>B. anay</i> *	Central America
					<i>B. costaricensis</i>	Central America, Andes
					<i>B. hexanthera</i>	French Guiana
					<i>B. immersinervis</i>	Central America
					<i>B. latifolia</i>	Andes
					<i>B. mexicana</i>	Central America
					<i>B. ovalioides</i>	Central America
					<i>B. ovalis</i>	Central America
					<i>B. pendula</i>	Central America, West Indies, northern South America, Andes
<i>B. curviramea</i> group	opposite	coarse	<i>B. curviramea</i> type	ring	<i>B. riparia</i>	Central America
					<i>B. steyermarkii</i>	Central America
					<i>B. tilaranensis</i>	Central America
					<i>B. tovarensis</i>	Central America, Andes
					<i>B. angustifolia</i>	Southeastern Brazil
					<i>B. curviramea</i>	Guianas
					<i>B. emarginata</i> *	Southeastern Brazil
					<i>B. fluminensis</i> *	Southeastern Brazil
					<i>B. linharensis</i>	Southeastern Brazil
					<i>B. rigida</i>	Southeastern Brazil
				<i>B. stricta</i> *	Southeastern Brazil	
				<i>B. taubertiana</i> *	Southeastern Brazil	
<i>B. hondurensis</i> group	opposite	coarse	<i>B. hondurensis</i> type	flattened arc	<i>B. angustieliptica</i>	Central America
					<i>B. brenesii</i>	Central America
					<i>B. hondurensis</i>	Central America
<i>B. miersii</i> group	opposite	coarse	<i>B. miersii</i> type	flattened arc	<i>B. manatlanensis</i> *	Central America
	opposite	coarse	<i>B. berteriana</i> type	flattened arc	<i>B. miersii</i>	Chile
<i>B. berteriana</i> group	opposite	coarse		flattened arc	<i>B. berteriana</i>	Chile



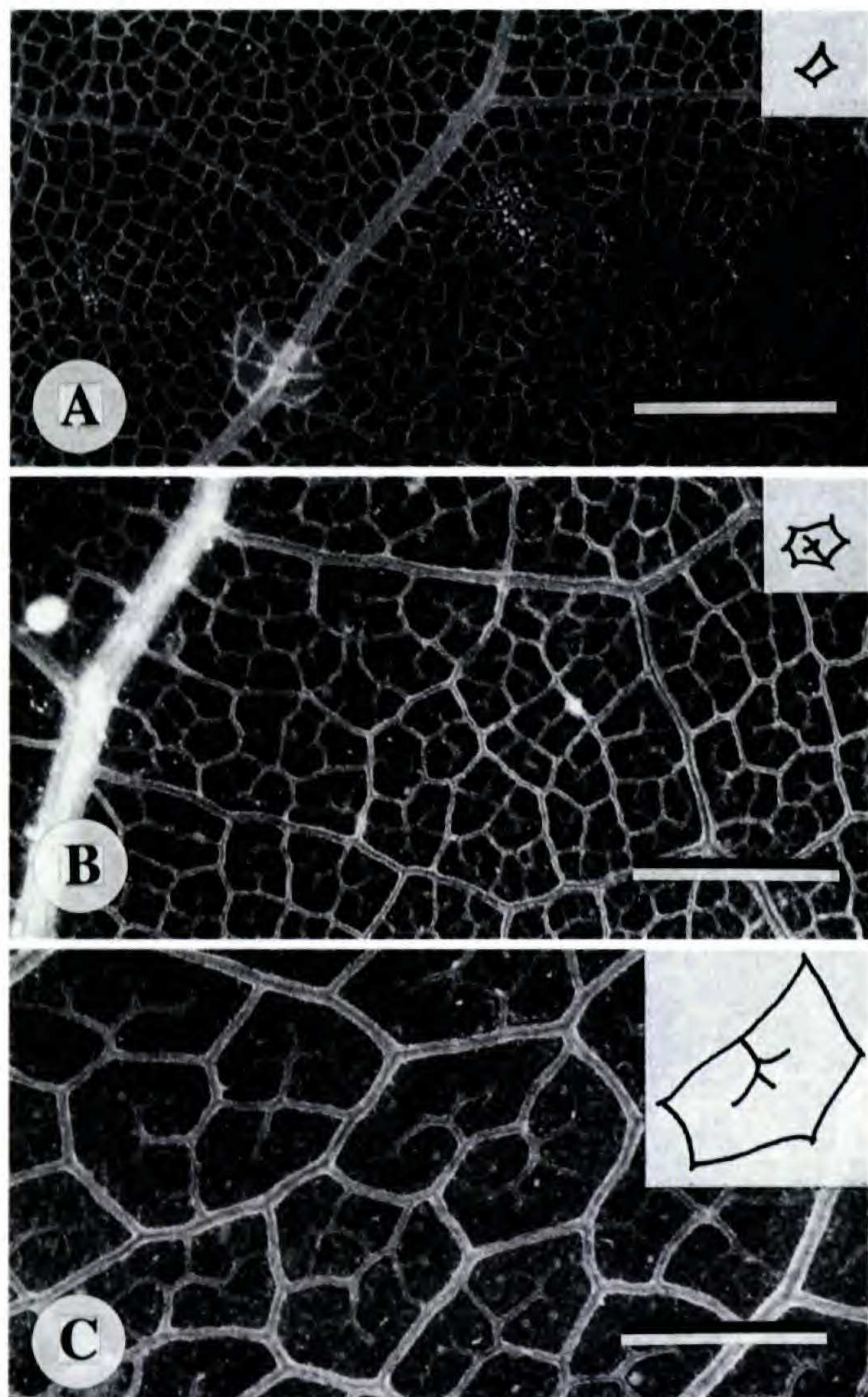


Figure 1. X-ray patterning for minor venation in neotropical *Beilschmiedia* species. —A. Fine, *B. mexicana* (Rubio 2209, MO). —B. Fine, *B. costaricensis* (Bello 4882, MO). —C. Coarse, *B. hondurensis* (Gentle 7292, MO). Line drawing in each corner = an areole. Scale bars = 2 mm.

(with branched, free-ending veinlets inside as in Fig. 1B) for species with a fine venation pattern. Veinlet pattern within areoles is usually branched (Fig. 1C) for species with a coarse venation pattern.

*Indumentum.* Indumentum can be used to delimit species, but it sometimes varies even within a spe-

cies. Hairs of neotropical *Beilschmiedia* species (Fig. 2) divide into three types by their orientation (appressed, ascending, erect) and straightness (straight, wavy, curly). Appressed hairs are always straight, appearing to be somewhat silky and shiny (Fig. 2A). Ascending hairs are also straight, but their orientation is looser than the appressed ones (Fig. 2B). Erect hairs can be straight, wavy, or curly (Fig. 2C, D, E, respectively). Minutely tomentulose pubescence with short curly hairs is sometimes referred to as “appressed” in treatises, but here it is classified as erect because the orientation is not basally appressed but erect. Straightness of the hairs sometimes varies on different parts of the plant. For example, hairs on inflorescences are usually erect even in the species with appressed hairs on the terminal buds and twigs. The orientation of hairs on terminal buds and twigs is usually stable enough to delimit the species, but hair straightness is relatively variable within species, especially in *B. alloiophylla* and *B. anay*.

*Inflorescences.* Inflorescences of neotropical *Beilschmiedia* species are mostly axillary and paniculate. They consist of a central axis with a number of alternately positioned lateral axes. The lateral axes are usually once- or twice-branched somewhat cymosely, but actually the ultimate divisions are not strictly cymose. This character distinguishes *Beilschmiedia* from most other large genera of Lauraceae in the Neotropics (except *Cryptocarya*), which have their ultimate inflorescence divisions strictly cymose.

In most species, inflorescence bracts are small, early-deciduous, and often absent at anthesis. Bract position is variable even within an inflorescence, with the length of pedicels above the bracts often varying within a species. Central elements of the ultimate inflorescence divisions usually have much longer floral pedicels than lateral elements. It is usually not practicable to use pedicel lengths to

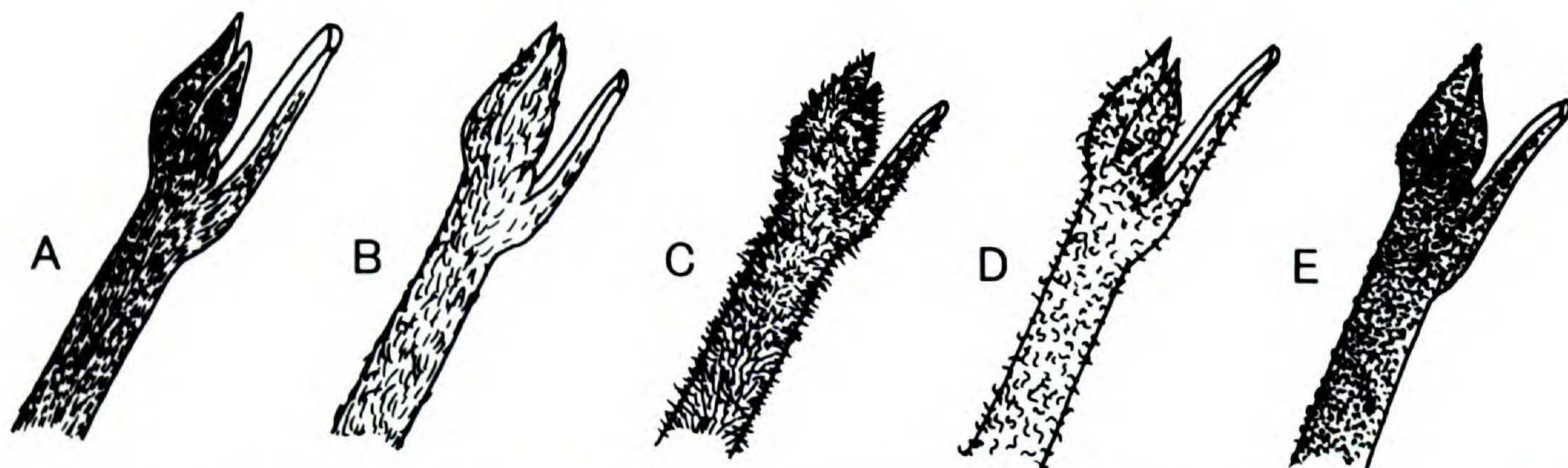


Figure 2. Five types of hairs in neotropical *Beilschmiedia* species. —A. Appressed. —B. Ascending. —C. Erect and straight. —D. Erect and wavy. —E. Erect and curly.



delimit species. However, some species, e.g., *B. brenesii*, have extremely long pedicels, and this character helps to distinguish that species from the others.

**Flowers.** Flowers are bisexual, small (ca. 3 mm long), and almost subspherical, except for those of *B. linharensis*, which are depressed-globose. Tepals are six, erect, almost equal, and usually ovate to elliptic. Stamens number nine in all neotropical *Beilschmiedia* species except for *B. hexanthera*, which has six. Anthers in the first and second whorls are ovate, and anthers in the third whorl are narrowly ovate to almost rectangular. Anther apices are obtuse to truncate in most species, but may be more or less acute in *B. angustieliptica*, *B. brenesii*, and *B. hondurensis*. Pubescence on anther apices distinguishes some species (*B. anay*, *B. angustifolia*, *B. curviramea*, *B. emarginata*, *B. fluminensis*, *B. linharensis*, *B. immersinervis*, *B. rigida*, *B. riparia*, *B. stricta*, and *B. taubertiana*) but, rarely, there are exceptional collections lacking this pubescence. Anther apices are glabrous in other species even if the anther sides are pubescent. Staminodia in the fourth staminal whorl are three in number and are conspicuous and sagittate or deltoid in shape. Staminodia in the third whorl in *Beilschmiedia hexanthera* are subulate in shape. Pistils are sometimes pubescent, but pubescence often varies within a species and may be easily overlooked. Receptacles are invariably shallow: this is a useful character to distinguish neotropical *Beilschmiedia* from *Cryptocarya*, in which the receptacle is deeply cupulate.

**Fruits.** Fruits are often ellipsoid in shape. *Beilschmiedia ovalis* and *B. ovalioides* have spherical fruits, and *B. anay* is reported to have pyriform fruits (Blake, 1919). Fruit color is usually black or purple-black at maturity.

Fruits of *Beilschmiedia* always lack cupules. Fruit pedicels are sometimes strongly constricted at their apices (Fig. 3A) or only weakly so (Fig. 3B); this is sometimes a useful character for species delimitation. In some species, e.g., *B. hondurensis* and *B. towarensis*, the pedicels are variable, ranging from constricted to not constricted (Fig. 3C).

**Cuticular characters.** Cuticular characters of neotropical *Beilschmiedia* species were studied by Nishida and Christophel (1999). According to them, neotropical *Beilschmiedia* species are hypostomatic, and the cuticular characters of the species can be divided into five types (Table 2; see also Fig. 4). For the species corresponding to each type, see Table 1.

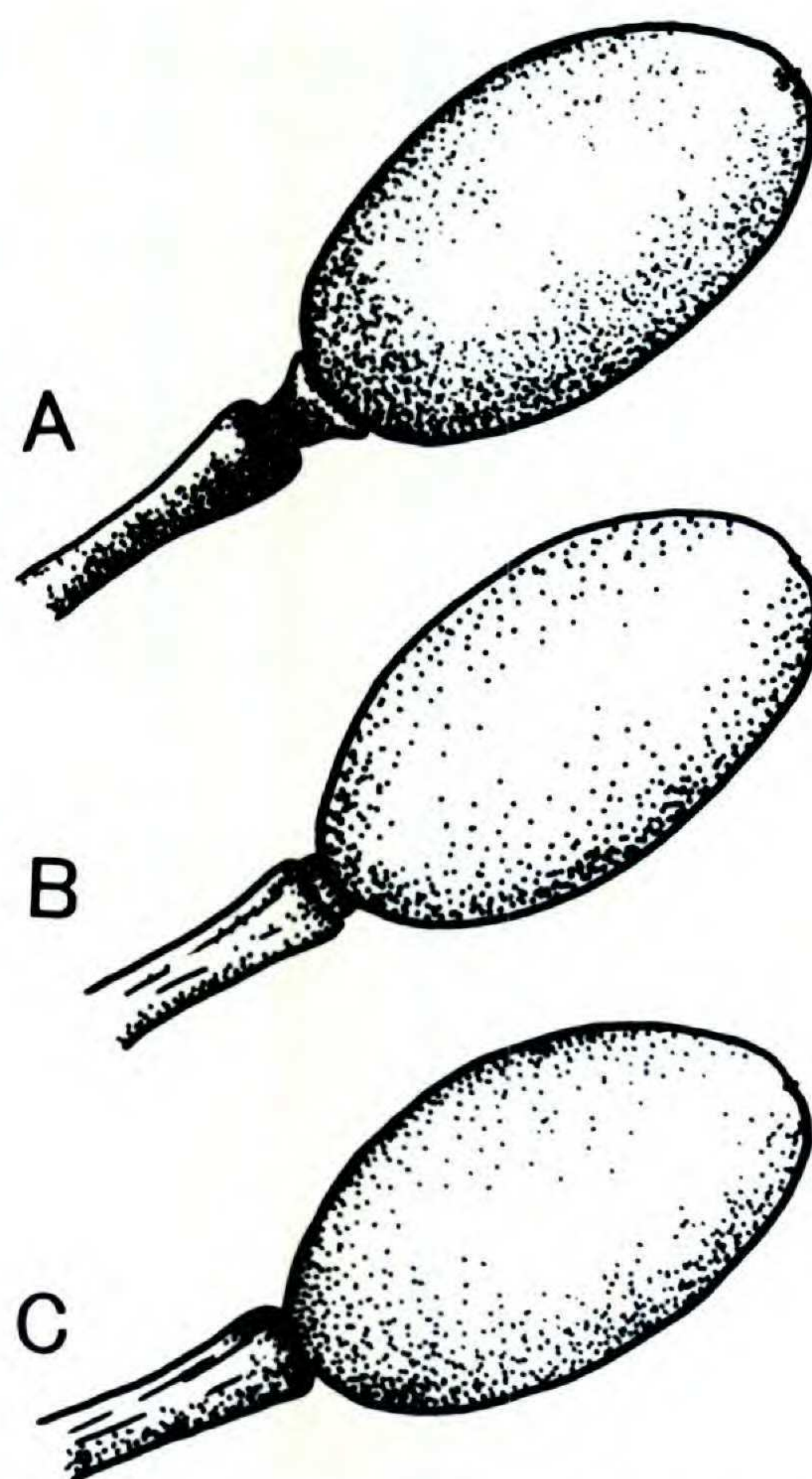


Figure 3. Fruits of neotropical *Beilschmiedia* species. —A. Fruit pedicel strongly constricted at the apex. —B. Fruit pedicel weakly constricted at the apex. —C. Fruit pedicel not constricted at the apex.

**Leaf cross sections.** Nishida and Christophel (1999) examined leaf sections of neotropical *Beilschmiedia* species, concluding that the most discriminating character was the arrangement of the vascular bundles in midribs. Two types are seen in neotropical *Beilschmiedia* species, one in a ring (Fig. 5A) and another in a flattened arc (Fig. 5B). For the species corresponding to each type, see Table 1.

#### DISTRIBUTION

In the Neotropics, *Beilschmiedia* ranges from central Mexico to southeastern Brazil and central Chile but is absent in the Amazon basin and northern Chile. Costa Rica has the highest number of species, with eight.

Many species range from tropical premontane wet forests to cloud forests. However, Chilean species are reported to occur in subtropical, semiarid vegetation (Heusser, 1971). Many species are distributed at lower and/or middle elevations. *Beilschmiedia latifolia*, *B. ovalioides*, and *B. ovalis* are also known from higher (1800–3000 m) elevations. *Beilschmiedia costaricensis* and *B. towarensis* occur over a wide range of elevation, 600–3000 m. No



Table 2. Five cuticular types of neotropical *Beilschmiedia*. Terminology used here is sensu Christophel et al. (1996) or Nishida and Christophel (1999).

	Epidermal cell walls			Dorsiventral differences in cell size	Stomatal ledge	Corresponding figures
	Periclinal walls	Anticlinal walls				
<i>B. costaricensis</i> type	smooth	smooth to beaded	absent to slightly present (adaxial $\leq$ abaxial)	narrow	4A, B	
<i>B. curvuramea</i> type	dotted (adaxial surface), granular (abaxial surface)	branched	absent	wide	4C, D	
<i>B. hondurensis</i> type	dotted	buttressed and strongly sinuous	absent	butterfly-shaped	4E, F	
<i>B. miersii</i> type	smooth	smooth to beaded	conspicuously present (adaxial $>$ abaxial)	narrow	4G	
<i>B. berteriana</i> type	smooth	smooth to beaded	absent	strongly swollen	4H	

reports are available on the altitudinal distribution of southeastern Brazilian species, but all of them are known from the Mata Atlantica region.

#### SEED DISPERSAL

Seeds of a few Costa Rican *Beilschmiedia* species are reported to be dispersed by birds such as quetzals (Wheelwright et al., 1984). Seeds remain in the bird's crop for more than an hour, while seeds of most of the other Lauraceae species remain there for a relatively short time (Wheelwright, 1995). Wheelwright (1986) also reported that fruit production varies greatly from year to year.

#### ECONOMIC USE

Some species, such as *Beilschmiedia latifolia*, *B. miersii*, and *B. pendula*, are useful as timber. Fruits of *B. anay* are reported to be edible by humans (Blake, 1919).

#### SYSTEMATIC POSITION IN LAURACEAE

*Beilschmiedia* had long been placed in the tribe Perseae Nees based on thyrsoid inflorescences without involucre. Kostermans (1957) regarded cupule development or its lack as an important character for lauracean systematics and placed *Beilschmiedia* close to genera such as *Endiandra*, *Mezilaurus*, *Potameia*, *Persea*, and *Phoebe*. Hutchinson (1964) regarded the number of anther cells as more important, placing *Beilschmiedia* in tribe Apollonieae Hutchinson with such genera as *Endiandra*, *Aniba*, *Mezilaurus*, *Licaria*, and *Endlicheria*.

Richter (1981) published wood and bark anatomy of Lauraceae, in which he recognized three large groups of genera. He placed *Beilschmiedia* in a group with *Endiandra*, *Potameia*, *Triadodaphne*, *Cryptocarya*, and *Ravensara*. Among these genera, *Cryptocarya* has fruits completely enclosed by cupules and has been regarded as a distantly related genus to *Beilschmiedia* by Kostermans (1957).

Van der Werff and Richter (1996) reviewed the classifications above and concluded that androecial characters such as the number of anther cells were not useful in a generic classification of Lauraceae. Instead, they proposed a classification based on inflorescence structure as well as wood and bark anatomy. In their study, *Beilschmiedia* was placed in the tribe Cryptocaryeae Nees and was distinguished by several characters such as paniculate inflorescences having the ultimate divisions not strictly cymose, parenchyma marginal, fibers non-septate with conspicuously bordered pits, and ves-



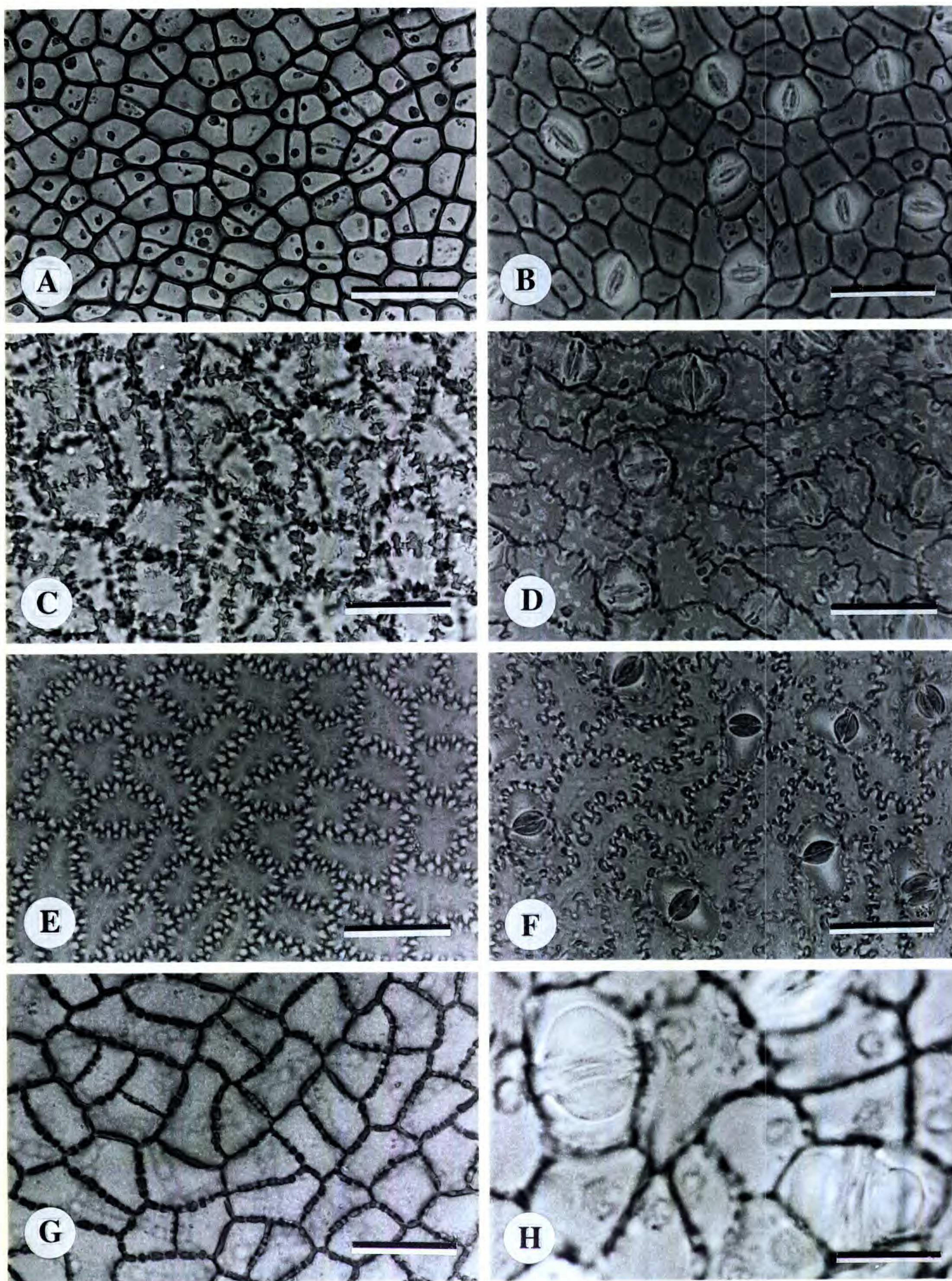


Figure 4. Cuticles of neotropical *Beilschmiedia* species on the adaxial (A, C, E, G) and abaxial leaf surfaces (B, D, F, H). —A, B. *B. costaricensis* (van der Werff 13368, 12168, respectively, MO). —C, D. *B. curviramea* (Persaud 70, NY). —E, F. *B. hondurensis* (Lundell 19280, MO). —G. *B. miersii* (Taylor 10883, MO). —H. *B. berteriana* (s.n., MO). Scale bars = 50 µm in A–G, 20 µm in H.



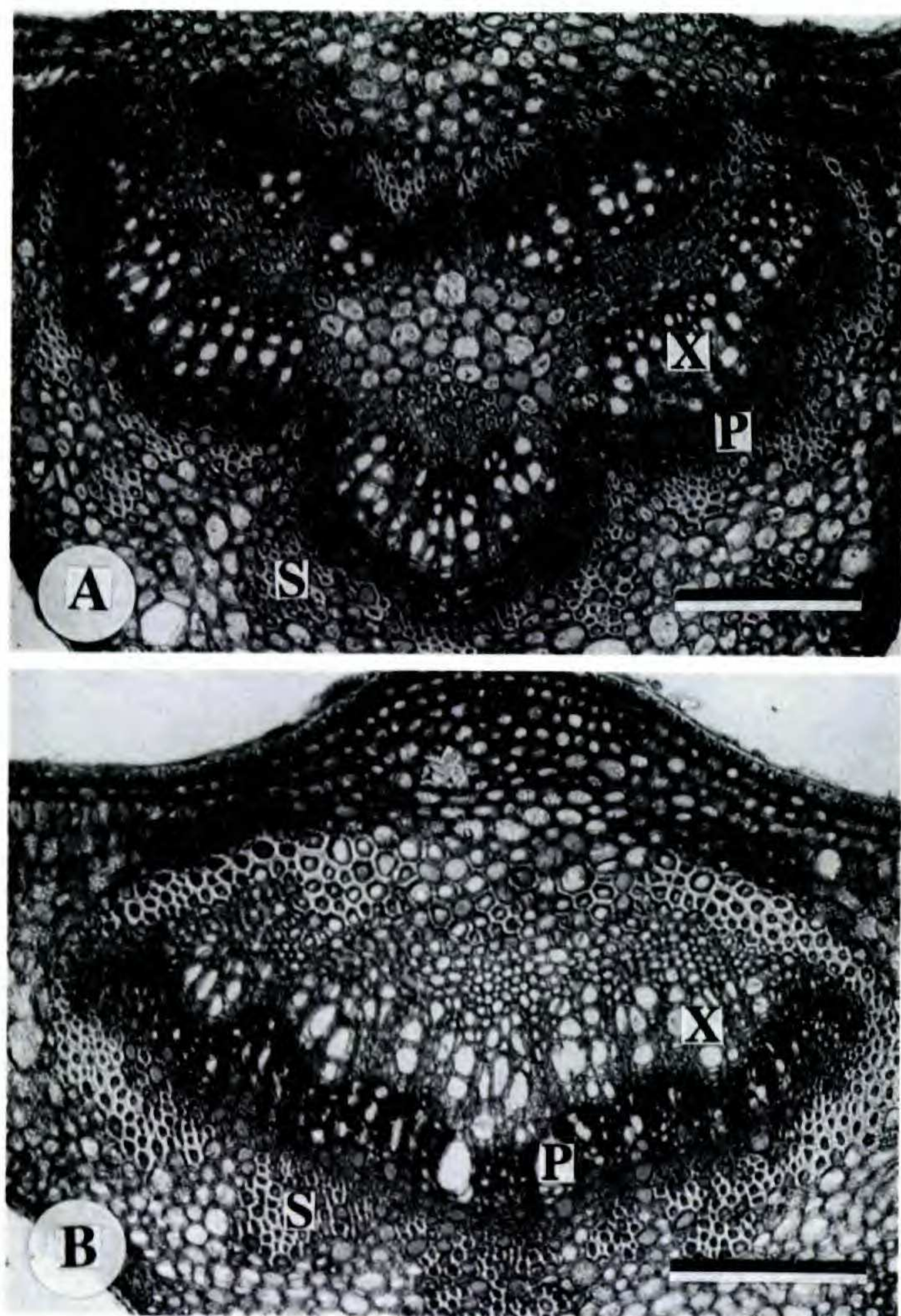


Figure 5. Leaf cross sections of neotropical *Beilschmiedia* through blade midribs. —A. Ring pattern, *B. mexicana* (Croat 64900, MO). —B. Flattened arc bundle pattern, *B. brenesii* (Yasuda 1314, MO). P = phloem, X = xylem, S = sclerenchymatous cells. Scale bars = 200  $\mu$ m.

sel perforations in secondary xylem exclusively simple.

Preliminary observations of different Lauraceae genera suggests that the genus closest to *Beilschmiedia* appears to be *Cryptocarya* in the Neotropics. Neotropical species of *Beilschmiedia* and *Cryptocarya* share morphological similarity except for the pistils being short or long, receptacles being shallow or deep, and fruits without cupules or enclosed by cupules, respectively. Further studies including molecular analysis may clarify relationships between these two genera, as well as the intergeneric relationships within Lauraceae.

#### RELATIONSHIPS AMONG NEOTROPICAL *BEILSCHMIEDIA* SPECIES

Neotropical *Beilschmiedia* species usually share quite similar flowers and fruits, and this makes it difficult to discuss their relationships based on reproductive characters. Nishida and Christophel

(1999) therefore employed leaf anatomy to investigate phylogenetic relationships. They concluded that the groupings of cuticular characters are systematically useful since they are also supported by phyllotaxis, leaf venation patterns, vascular bundle arrangements in blade midribs, and by rough geographical distributions. These species groupings are listed in Table 1 but should be considered informal until the entire genus has been revised.

These five species groups can be recognized even without examining the cuticular characters. First, all neotropical *Beilschmiedia* species with alternate leaves and a fine leaf venation pattern belong to the *Beilschmiedia costaricensis* group. Among other species, those with anthers apically pubescent and distributed in southeastern Brazil or the Guianas belong to the *Beilschmiedia curviramea* group. Mexican or Central American species whose leaves are opposite and anther apices are relatively acute belong to the *Beilschmiedia hondurensis* group. Finally, of the two Chilean species, the one with curly hairs on the twigs belongs to the *Beilschmiedia miersii* group, while the second has straight hairs on the twigs and belongs to the *Beilschmiedia berteriana* group.

#### TAXONOMIC TREATMENT

***Beilschmiedia*** Nees, in Wallich, *Pl. Asiat. Rar.* 2: 61, 69. 1831. TYPE: *Beilschmiedia roxburghiana* Nees.

*Hufelandia* Nees, *Plantarum Laurinarum Secundum Affinitates Naturales Expositio*: 11. 1833. TYPE: *Hufelandia pendula* Nees.

*Bellota* Gay, *Fl. Chil.* 5: 297. 1851 or 1852. TYPE: *Bellota miersii* Gay.

Trees or rarely shrubs. Leaves alternate or opposite, rarely clustered, pinnately veined. Inflorescences in leaf axils, paniculate or racemose, with terminal branches of the panicles not strictly cymose. Flowers bisexual; tepals 6, equal or subequal, usually deciduous; stamens 9 or 6, filaments usually shorter than the anthers; anthers usually 2-celled, first and second whorls introrse, third whorl extrose to almost introrse, staminodia 3 in fourth whorl or absent, or rarely 6 in third and fourth whorls, staminodia representing third whorl subulate, staminodia representing fourth whorl sagittate or deltoid; ovary superior; receptacle flat to shallowly cupulate. Fruit ellipsoid, pyriform or spherical, usually purple-black, lacking cupule.



KEY TO NEOTROPICAL *BEILSCHMIEDIA* SPECIES

- 1a. Leaves opposite (the top leaves opposite even when leaves clustered); minor venation pattern on lower leaf surface coarse, areoles (smallest areas of the leaf tissue surrounded by veins) larger than 1.5 mm diam. (Fig. 1C).
- 2a. Anther apices glabrous; from Central America or Chile.
- 3a. Leaves roundish ovate; from Chile.
- 4a. Tepals glabrous outside; hairs on the terminal buds and twigs appressed or ascending, straight ..... *B. berteroa*
- 4b. Tepals pubescent outside; hairs on the terminal buds and twigs erect, curly to wavy ..... *B. miersii*
- 3b. Leaves elliptic or narrowly obovate; from Central America.
- 5a. Terminal buds pubescent with erect hairs; young twigs densely pubescent; secondary veins more than 14 pairs.
- 6a. Leaves clustered; leaf apices roundish to obtuse; filament of innermost stamens relatively densely pubescent ..... *B. manantlanensis*
- 6b. Leaves evenly arranged; leaf apices acute; filament of innermost stamens only sparsely pubescent ..... *B. angustilipica*
- 5b. Terminal buds pubescent with appressed or ascending hairs; young twigs glabrous; secondary veins less than 13 pairs.
- 7a. Floral pedicels shorter than 2 mm; from Mexico to Honduras ..... *B. hondurensis*
- 7b. Floral pedicels longer than 3 mm; from Costa Rica and Panama ..... *B. brenesii*
- 2b. Anther apices pubescent; from northern South America or southeastern Brazil.
- 8a. Lower leaf surface pubescent; leaf base obtuse ..... *B. taubertiana*
- 8b. Lower leaf surface glabrous; leaf base cuneate.
- 9a. Hairs on the terminal buds and twigs ferruginous, erect, very short and curly ..... *B. emarginata*
- 9b. Hairs on the terminal buds and twigs non-ferruginous, appressed, relatively long and straight.
- 10a. Leaves obovate; leaf apex round or roundish obtuse.
- 11a. Flowers longer than 3 mm, wider than 3 mm; flowers globose ..... *B. rigida*
- 11b. Flowers shorter than 2 mm, narrower than 2.5 mm; flowers depressed-globose ..... *B. linharensis*
- 10b. Leaves elliptic; leaf apex acute (rarely obtuse).
- 12a. Leaf width less than  $\frac{1}{3}$  of the leaf length ..... *B. angustifolia*
- 12b. Leaf width more than  $\frac{1}{2}$  of the leaf length.
- 13a. Inflorescences racemose,  $\pm$  densely pubescent ..... *B. stricta*
- 13b. Inflorescences paniculate, sparsely pubescent or almost glabrous.
- 14a. Leaf base slightly inrolled; from southeastern Brazil ..... *B. fluminensis*
- 14b. Leaf base flat; from northern South America ..... *B. curviramea*
- 1b. Leaves alternate, spirally clustered, rarely subopposite; minor venation pattern usually fine, areoles smaller than 0.5(-0.7) mm diam. (Fig. 1A, B); when venation pattern relatively coarse, leaves still alternate and from Ecuador or Colombia (*B. costaricensis*).
- 15a. Fertile stamens 6; staminodia 6; from French Guiana ..... *B. hexanthera*
- 15b. Fertile stamens 9; staminodia 3; from Central America, West Indies, or western South America.
- 16a. Hairs on terminal buds and twigs appressed (Fig. 2A) or ascending (Fig. 2B); when hairs ascending, minor venation pattern slightly less fine, areoles around 0.7 mm diam. (*B. costaricensis*).
- 17a. Leaves glaucous below.
- 18a. Areoles angular with branched free-ending veinlets inside (Fig. 1B); fruit pedicels strongly constricted (Fig. 3A) ..... *B. pendula*
- 18b. Areoles rounded, seldom with free-ending veinlets inside (Fig. 1A); fruit pedicels weakly constricted (Fig. 3B), rarely not constricted (Fig. 3C).
- 19a. Leaves chartaceous; from Mexico to Belize ..... *B. mexicana*
- 19b. Leaves usually coriaceous; from northwestern South America to Costa Rica ..... *B. towarensis*
- 17b. Leaves not glaucous below.
- 20a. Areoles angular with branched free-ending veinlets inside; fruit pedicels not constricted (Fig. 3C); from northwestern South America to Costa Rica ..... *B. costaricensis*
- 20b. Areoles rounded seldom with free-ending veinlets inside (Fig. 1A); fruit pedicels weakly constricted (Fig. 3B); from Mexico to Belize ..... *B. mexicana*
- 16b. Hairs on terminal buds and twigs erect (Fig. 2C-E).
- 21a. Anther apices pubescent.
- 22a. Petioles longer than 2.5 cm; leaves longer than 18 cm, wider than 11 cm ..... *B. anay*
- 22b. Petioles shorter than 2 cm; leaves shorter than 16.5 cm, narrower than 7.5 cm.
- 23a. Secondary veins conspicuously raised below; lower leaf surface not glaucous; from Mexico, south to Nicaragua ..... *B. riparia*



- 23b. Secondary veins immersed below (visible); lower leaf surface glaucous; from Costa Rica ..... *B. immersinervis*
- 21b. Anther apices glabrous.
- 24a. Leaves narrowly elliptic, the width less than 4 cm and less than  $\frac{1}{2}$  of the length ..... *B. steyermarkii*
- 24b. Leaves broadly elliptic, ovate or obovate, the width more than 4 cm and more than  $\frac{1}{2}$  of the length.
- 25a. Lower leaf surface glabrous when old.
- 26a. Leaves longer than 22 cm ..... *B. alloiophylla*
- 26b. Leaves shorter than 13 cm.
- 27a. Leaves ovate; tertiary veins weakly percurrent or reticulate; inflorescences relatively densely pubescent; fruits spherical ..... *B. ovalis*
- 27b. Leaves obovate; tertiary veins strongly percurrent; inflorescences glabrous or sparsely pubescent; fruits ellipsoid ..... *B. tilaranensis*
- 25b. Lower leaf surface pubescent when old.
- 28a. From Mexico; fruits spherical ..... *B. ovalioides*
- 28b. From southern Central America (Costa Rica, Panama) or western South America; fruits ellipsoid.
- 29a. Leaves ovate to broadly elliptic; leaves shorter than 11 cm; secondary veins less than 9 pairs ..... *B. latifolia*
- 29b. Leaves obovate (rarely broadly elliptic); leaves longer than 22 cm; secondary veins more than 9 pairs ..... *B. alloiophylla*

1. ***Beilschmiedia alloiophylla*** (Rusby) Kosterm., Rec. Trav. Bot. Néerl. 35: 849. 1938. *Ocotea alloiophylla* Rusby, Descr. S. Amer. Pl.: 21. 1920. TYPE: Colombia. Santa Marta: mountain forest 5 mi. SE of Don Amo, ca. 750 m, 7 Mar. 1898–1901 (young fl), *H. H. Smith 2104* (lectotype, designated by Kostermans (1938), NY not seen; isolectotypes, A not seen, BM!, G-DEL not seen, K!, MO!, P!, US not seen).

Tree, to 35 m tall. Terminal buds densely pubescent with erect, short to long, straight to curly hairs. Twigs terete, sometimes sulcate or angular, sometimes corky, densely pubescent with erect, short to long, straight to curly hairs. Leaves clustered, rarely almost alternate; petioles 0.7–3.5(–4.5) cm long, canaliculate to flat above, pubescent with erect, short to long, straight to wavy hairs, concolorous with twigs; blades firmly chartaceous, elliptic to obovate, (14–)22–30 × 6–13(–17) cm; base cuneate or obtuse, not inrolled or rarely inrolled, apex acute to acuminate; upper leaf surface glabrous (sometimes pubescence left mainly on midrib when young), lower leaf surface pubescent with erect to almost appressed, short to long, straight to curly hairs, or glabrous, rarely pubescent only on major veins; lower leaf surface glaucous; midrib and secondary veins slightly impressed or immersed above, raised below, secondary veins 9 to 16 (19) pairs, tertiary veins percurrent, minor venation pattern fine, areoles rounded and seldom with free-ending veinlets inside, tertiaries and minor veins almost immersed (the pattern poorly visible) or slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, (4–)8–25 cm long, pubescent

with erect, wavy hairs, with (30) 60 to 250 or more flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 2 mm long. Flowers green to creamy, ca. (2–)2.2–3 mm long, ca. 2 mm diam.; tepals 6, equal, ovate to elliptic, 1.5–2.1 × 1–1.5 mm, pubescent with erect and wavy hairs on both surfaces; stamens 9, filaments 0.4–0.5 mm long, pubescent, anthers 0.6–0.7 mm long, 2-celled, anther apices roundish to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1–1.7 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purple-black, 3.5–4.5 × 1.5–2.5 cm, surface smooth; infructescence axis 2.5–3 mm diam., slightly thickened to 4 mm diam. near the fruit pedicel, fruit pedicels apically constricted, or rarely not constricted.

*Flowering time.* January to July.

*Distribution and habitat.* Costa Rica, Panama, western Venezuela, western Colombia, and Ecuador (Fig. 6); (35–)100–1400(–1900) m; evergreen lowland forest, premontane wet forest and montane wet forest.

*Common names.* Jigua de aguacate (*Dodson & Gentry 6489*), María aguacatillo (*Josse et al. 843*) (Ecuador).

*Selected specimens examined.* COSTA RICA. **Cartago:** Cartago Province, on slopes above Muñeco, 1550 m, 19 Mar. 1986 (fr), *Almeda et al. 5639* (MO). **Guanacaste:** Parque Nacional Guanacaste, La Cruz, Estación Pitilla, 10°59'26"N, 85°25'40"W, 700–1000 m, 1 Apr. 1991 (fl), *Morega 337* (INB, MO). **Heredia:** Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its



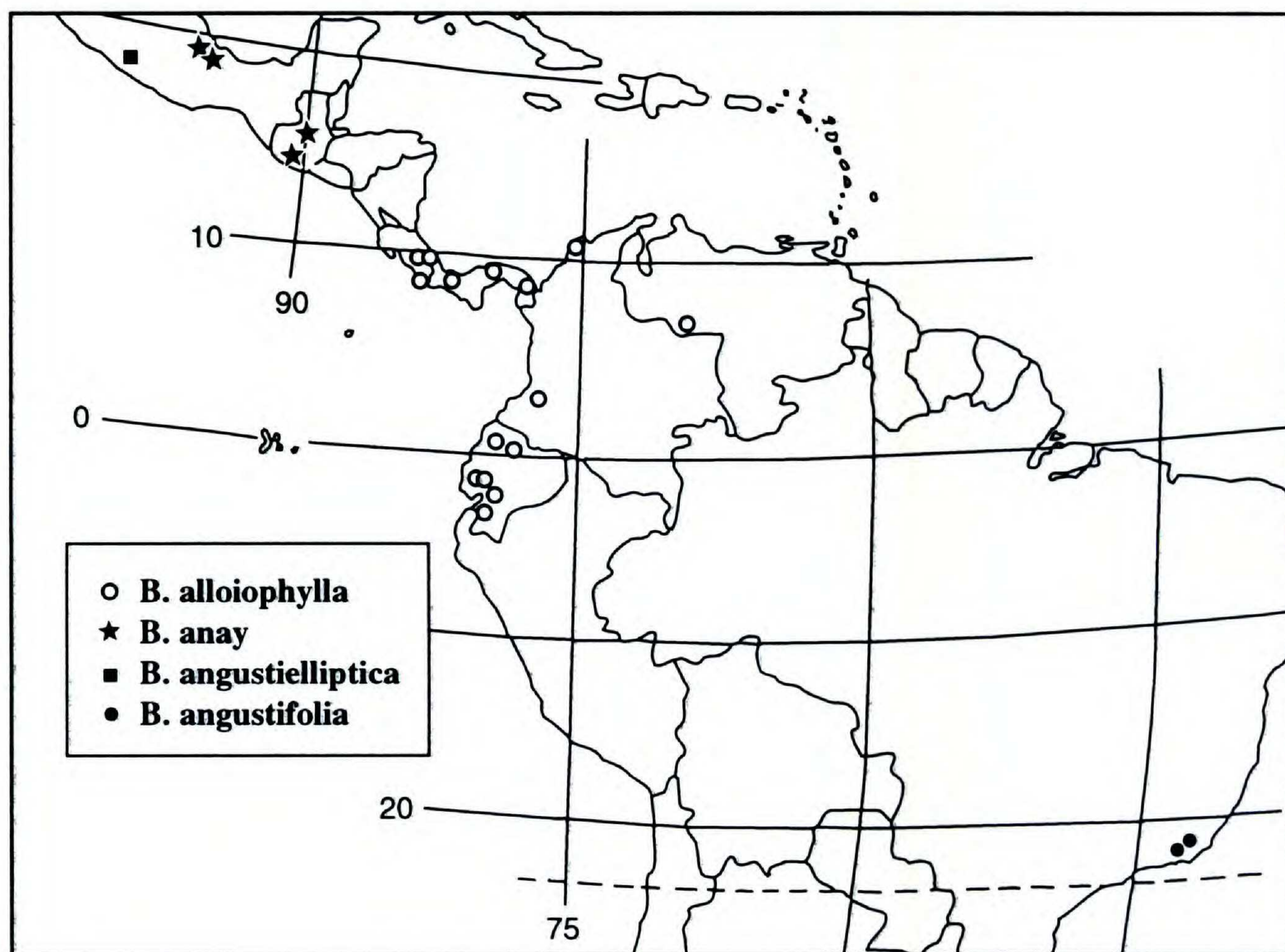


Figure 6. Representative distribution of *Beilschmiedia alloiophylla*, *B. anay*, *B. angustielliptica*, and *B. angustifolia*.

junction with the Río Sarapiquí, 100 m, 25 July 1981 (fl), *Hammel 11049* (MO, NY). **Limón:** SE region of Lago Dabagrí, cross the road to Telire, 5 Nov. 1984 (fr), *L. D. Gómez et al. 23216* (CR). **Puntarenas:** Cantón de Golfito, Corcovado National Park, Sendero Los Patos, 8°34'00"N, 83°31'00"W, 200 m, 6 June 1994 (young fl), *Aguilar 3346* (INB, MO). **San José:** along Quebrada Tablazo and on slope S of creek, NE slope of Altos Tablazo, 9°50'N, 84°03'W, 1675–1900 m, 24 Apr. 1987 (immature fr), *Grayum et al. 8263* (CR, R, MO). **PANAMA. Bocas del Toro & Chiriquí:** Cerro Colorado, from Chami station to ca. 9 mi. along road, 8°35'N, 81°54'W, 1100–1750 m, 27–31 Mar. 1986 (fr), *Hammel & Trainer 14992* (MO). **Darién:** Río Pirre, 16 Nov. 1967 (fr), *Bristan 1472 (4)* (MO). **Panamá:** Cerro Jefe, along summit road and along trail into Chagres Valley, 9°15'N, 79°30'W, 900 m, 19 Feb. 1988 (fl), *McPherson 12122* (MO). **VENEZUELA. Mérida:** Sierra de Perijá, Misión Sabana, 1300 m, 22 Mar. 1959 (young fl), *Bernardi 7452* (K, NY). **COLOMBIA. Valle:** Cordillera Occidental, La Laguna, Río Sanquinín basin, 1250–1400 m, 10–20 Dec. 1943 (fr), *Cuatrecasas 15619* (F). **ECUADOR. Azuay:** Cantón Cuenca, Parroquia Molleturo, Manta Real, 02°34'S, 79°23'W, 300–1200 m, 28 July 1992 (immature fr), *Berg 46* (MO). **El Oro:** road between Santa Rosa & Portovelo, 25 Mar. 1921 (immature fr), *Popenoe 1304* (US). **Esmeraldas:** Quininde, Bilsa Biological Station, Mache Mountains, 35 km W of Quininde, 5 km W of Santa Isabel, 0°21'N, 79°44'W, 400–600 m, 14 Nov. 1994 (young fl), *Clark & Pitman 248* (MO). **Guayas:** Cordillera Chongon-Colonche, Loha Alta Protected Forest, 1°48'S, 80°47'W, 600 m, July 1995 (immature fr), *Bonifaz & Cornejo 3091* (MO). **Los Ríos:** 56

km of Quevedo-Santo Domingo, Río Palenque Biological Station, 150–220 m, 25 Mar. 1980 (sterile), *Dodson & Gentry 9906* (MO). **Manabí:** Parque Nacional Machalilla, Piñas to the hill Avión Caído, 01°35'S, 80°41'W, 300 m, 13 Sep. 1991 (fr), *Josse 714* (MO). **Pichincha:** along road Nanegal–Palmitopamba, 1200 m, 9 July 1991 (immature fr), *van der Werff 12256* (MO).

*Beilschmiedia alloiophylla* belongs to the *B. costaricensis* group. This species is distinguished by the following: hairs erect on terminal buds and twigs, leaves alternate, large and obovate, anthers glabrous, and fruits ellipsoid.

*Beilschmiedia alloiophylla* is a complex species with variable indumentum. Collections recognized here as this species roughly separate into five groups based mainly on the hair structure and the amount of pubescence.

Group 1 species have short to long, straight to curly hairs on terminal buds and twigs, with long straight hairs on the tissue of lower leaf surfaces. Collections identified to this group include many Ecuadorian ones, all Colombian ones (including the type), all Venezuelan ones, as well as one Panamanian one. Altitudinal distribution of this group is usually around 1200 m elevation. A few collections occur lower than 300 m.

Group 2 species display short, curly hairs on ter-



minal buds and twigs, with sparse, sericeous hairs or almost no hair on lower leaf surfaces. Petioles in this group are often shorter than those of other groups. This group has been collected mainly from relatively low elevations (150–600 m) on the Pacific coast of Ecuador. Distributions overlap between this species group and Group 1.

Group 3 features long straight hairs on terminal buds, twigs, and major veins of abaxial blade surfaces. Lower leaf surfaces in this group have dense hairs only along the blade midribs and secondary veins. Only one collection, *McPherson 12122* from Panama at 900 m, belongs to this group.

Group 4 species are characterized by short curly hairs on terminal buds and twigs but almost no hair on lower blade surfaces. There are occasional curly hairs on major veins when the leaves are young. This group has been collected from 700 to 1900 m in Costa Rica and Panama (with one collection, *Hammel 11049*, found at ca. 100 m in Costa Rica). Burger and van der Werff (1990) regarded them as a larger-leaved variation of *B. ovalis*, but they can be reliably separated from *B. ovalis* by their strongly percurrent tertiary veins and ellipsoid fruits.

Group 5 species have short curly hairs on terminal buds, twigs, and lower leaf surfaces. Lower leaf surfaces may be sparsely pubescent to almost glabrous. This group has been collected only from lower elevations (below 350 m) on the Osa Peninsula, Costa Rica.

**2. *Beilschmiedia anay*** (S. F. Blake) Kosterm., *Rec. Trav. Bot. Néerl.* 35: 847. 1938. *Hufelandia anay* S. F. Blake, *J. Wash. Acad. Sci.* 9: 459. 1919. TYPE: Guatemala. Suchitepéquez: Mazatenango, Finca Compromiso, ca. 420 m, 17 Jan. 1917 (immature fr), *Popenoe 754* (holotype, US!; isotype, US!).

Tree, to 40 m tall. Twigs terete to sulcate, densely pubescent with erect, curly to wavy or rarely almost straight hairs, rarely not so densely pubescent, rarely glabrescent with age. Leaves alternate, rather clustered around the terminal buds; petioles 2.5–4 cm long, canaliculate to flat above, pubescent with erect, wavy or almost straight hairs, concolorous with twigs; blades chartaceous, broadly elliptic to ovate, (14–)18–28 × 11–15 cm; base obtuse to rounded, rarely cuneate, not inrolled, apex acute, rarely cuspidate; upper leaf surface glabrous, or sometimes pubescent with wavy hairs along the midrib, lower leaf surface pubescent with erect, short curly hairs or long wavy hairs, especially densely pubescent along the midrib and secondary veins; lower leaf surface often glaucous; midrib and

secondary veins immersed or slightly impressed above, raised below, secondary veins 12 to 17 pairs, tertiary veins percurrent, minor venation pattern fine, areoles rounded and seldom with free-ending veinlets inside, tertiaries and minor veins immersed above (pattern partially visible), slightly raised or almost immersed below (the pattern visible), the venation pattern visible on upper leaf surface much coarser than on lower leaf surface. Inflorescences axillary, sometimes crowded near the terminal buds, paniculate, 5–10 cm long, pubescent with erect, curly to wavy hairs, with 30 to 70 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 4 mm long. Flowers yellowish, 2.5–3.2 mm long, 2.8–3.5 mm diam.; tepals 6, equal, elliptic, ca. 2 mm long, 1–1.6 mm wide, ± densely pubescent with erect, wavy hairs on both sides; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments 0.4–0.7 mm long, filaments pubescent, anthers 0.8–1 mm long, 2-celled, anther apices roundish to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.6–0.8 mm long; pistil 1.3–1.6 mm long, glabrous, ovary as long as or longer than and gradually narrowed into the style; receptacle pubescent with ± appressed hairs. Fruits ellipsoid to pyriform, deep purple to black, to ca. 15 cm long (fide Blake, 1919); fruit pedicels unknown.

*Flowering time.* April and May.

*Distribution and habitat.* Eastern Mexico and Guatemala (Fig. 6); 100–920 m; montane mesophyll forest and deciduous forest, on loamy, clayish soil or limestone.

*Common names.* Anay (Guatemala); Anaya negra/Jani'ya (*G. Villalobos C. & Guerrero 138*) (Mexico).

*Selected specimens examined.* MEXICO. **Puebla:** Municipio Xochitlán de Vicente Suárez, 19°58'N, 97°44'W, 850 m, 22 Nov. 1987 (fr), *G. Villalobos C. & Guerrero 244* (MEXU). **Veracruz:** entre Maratinez de la Terre & Misantla, 100 m, 21 Oct. 1967 (sterile), *Pennington & Sarukhán 9265* (NY). GUATEMALA. **Alta Verapaz:** Chamá, ca. 270 m, 6 May 1920 (fl), *Johnson 170* (F, MO, U, US). **Escuintla:** Río Guacalate, 600 m, 16 Dec. 1938 (young fl), *Standley 60223* (F).

Kostermans (1938) reported *Beilschmiedia anay* from Guatemala, Costa Rica, and Colombia. However, he stated that he was not sure if Costa Rican specimens seen belonged to *B. anay*, and that the Colombian specimen seen had almost glabrous leaves, atypical for *B. anay*. I have not seen the specimens he cited, nor any specimen of *B. anay* from Costa Rica or Colombia. All the specimens I



recognize as *B. anay* are from Guatemala or Mexico.

*Beilschmiedia anay* appears to be vegetatively similar to *B. alloiophylla*. However, *B. anay* differs from *B. alloiophylla* by its pubescent anthers.

*Beilschmiedia anay* is reported to have pyriform fruits (Blake, 1919), differing from the elliptic or spherical fruits observed for most neotropical *Beilschmiedia* species. However, I have not seen good fruiting collections of *B. anay*, only ones with very young or detached fruits. Fruit characters for this species should be confirmed through the collection of relevant material.

**3. *Beilschmiedia angustieliptica*** Lorea-Hern., Novon 5: 47. 1995. TYPE: Mexico. Guerrero: Municipio Atoyac de Alvarez, ca. 2 km S to El Molote, on the trail to El Edén, 1580 m, 19 May 1993 (fl & fr), Lorea & Lozada 5540 (holotype, FCME not seen; isotype, MO!).

Tree, 7–8 m tall. Terminal buds pubescent with yellowish brown to reddish brown, erect wavy hairs. Twigs terete, compressed when young, densely pubescent with erect, long wavy hairs, becoming less dense to glabrescent with age. Leaves opposite, rarely subopposite; petioles 0.7–1.7 mm, flat or slightly canaliculate above, pubescent with erect wavy hairs but soon glabrous, concolorous with twigs or slightly discolored from twigs; blades firmly chartaceous, narrowly elliptic, margin sometimes slightly undulate, (7–)12–20(–24) × 2–6 cm, base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 13 to 22 pairs, slightly raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets, tertiaries and minor veinlets slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, 2.5–6(–10) cm, pubescent with erect hairs, with 30 to 60 flowers per inflorescence; floral pedicels of the lateral divisions 1.2–2 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2–2.7 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate, 1.3–1.7 mm long, 0.9–1.3 mm wide, outside pubescent with erect hairs, inside sparsely pubescent with appressed to erect hairs; stamens 9, outer six with filaments ca. 0.4 mm, innermost three with filaments ca. 0.5 mm long, all filaments sparsely pubescent, outer six with anthers 0.6–0.8 mm long, innermost three with anthers ca. 0.5 mm long, 2-celled, apex of the outer six anthers roundish to acute, apex of the innermost three anthers truncate, apex of all the anthers gla-

brous, glands of the innermost three stamens globose; staminodia 3, sagittate, 0.4–0.6 mm long; pistil ca. 1.2 mm long, glabrous or slightly pubescent, ovary slightly longer than and gradually narrowed into the style or sometimes the border between ovary and style conspicuous; receptacle pubescent with ± erect hairs, less densely pubescent toward the bottom. Fruits ellipsoid, black, 2.5–3.5 × 1.5–1.7 cm, surface smooth; infructescence axis 1.5–2 mm diam., slightly thickened to 3 mm diam. near fruit pedicels, with fruit pedicels constricted at apices.

*Flowering time.* May.

*Distribution and habitat.* Guerrero, Mexico (Fig. 6), at 1360–1630 m in mesophyllous montane forest.

*Selected specimen examined.* MEXICO. Guerrero: Municipio Atoyac de Alvarez, El Molote, 1630 m, 15 Apr. 1984 (fr), Núñez 1159 (MO).

Among Mexican species, *Beilschmiedia angustieliptica* is distinguished by its opposite, evenly arranged, long leaves. Lorea-Hernández (1995) considered ovary pubescence as a distinctive character for this species. However, I have observed that some ovaries in this species are glabrous or only sparsely pubescent so that one can easily miss the pubescence.

**4. *Beilschmiedia angustifolia*** Kosterm., Rec. Trav. Bot. Néerl. 35: 857. 1938. TYPE: Brazil. Rio de Janeiro: Ad cataractam Vargem, Teresopolis, Serra dos Orgãos, 2 Feb. 1838 (fr), Miers s.n. (holotype, BM!).

Tree, to 10 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely pubescent with appressed straight hairs or almost glabrous. Leaves opposite; petioles 0.7–1.3(–1.8) cm long, flat above, glabrous, concolorous with twigs; blades firmly chartaceous, narrowly elliptic, 7–14 × 1.5–4 cm, base acute, slightly inrolled toward the lower surface, apex acute; leaf surface glabrous on both sides; unknown whether lower leaf surface is glaucous or not; midrib immersed above, raised or almost immersed below, secondary veins 9 to 14 pairs, slightly raised or almost immersed on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed on both sides. Inflorescences in axils of leaves, paniculate with few branches, 2–3.5 cm long, sparsely pubescent with appressed to erect hairs, with 10 to 15 flowers per inflorescence; floral pedicels of the



lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm diam.; tepals 6, equal, ovate, 1.3–1.7 mm long, ca. 1.3 mm wide, pubescent with appressed to erect hairs outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, all filaments pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices roundish to truncate and pubescent, glands on the innermost three stamens globose, ca. 0.4 mm long; staminodia 3, sagittate, ca. 0.5 mm long; pistil ca. 1.8 mm long, pubescent, ovary as long as the style, the border between ovary and style  $\pm$  clear; receptacle pubescent with appressed hairs, less densely pubescent toward the bottom. Fruits roundish ellipsoid, ca. 3  $\times$  ca. 2.7 cm, surface smooth; infructescence axis ca. 3 mm diam., fruit pedicels slightly thickened to 4–7 mm diam. below the fruit, not constricted.

*Flowering time.* October and November.

*Distribution.* Rio de Janeiro, Brazil (Fig. 6).

*Common name.* Tapinhao (Kostermans, 1938).

*Selected specimen examined.* BRAZIL. **Rio de Janeiro:** Vista Chinesa, 13 Oct. 1925 (fl), *Constantino 19914* (RB).

Among southeastern Brazilian species, *Beilschmiedia angustifolia* is distinguished by its narrowly elliptic leaves. The widths of the leaves in *B. angustifolia* are usually  $\frac{1}{4}$ , at most  $\frac{1}{3}$ , of blade lengths, while blade widths in most other southeastern Brazilian species correspond to  $\frac{1}{2}$  the length or more. *Beilschmiedia taubertiana* also tends to have narrow leaves; these are not narrower than  $\frac{1}{3}$  of blade lengths, and the erect pubescence of its terminal buds, twigs, and lower leaf surfaces distinguish this species from *B. angustifolia*.

In addition to its narrow leaves, *B. angustifolia* has pubescent pistils, which are characteristic only for this species and *B. rigida* among southeastern Brazilian species.

**5. *Beilschmiedia berteriana*** (Gay) Kosterm., *Rec. Trav. Bot. Néerl.* 35: 858. 1938. *Cryptocarya berteriana* Gay, *Fl. Chil.* 5: 301. 1851 or 1852. TYPE: Chile. Mts. La Leona, Nov. 1829 (fl & immature? fr), *Bertero s.n.* (lectotype, designated by Kostermans (1938), P!; is-lectotypes, G-DEL not seen, P!, GH not seen, W not seen).

*Bellota nitida* Phil., *Linnaea* 29: 39. 1857–1858. *Boldu nitidum* (R. A. Philippi) Meisn., in DC., *Prodr.* 15(1): 506. 1964. TYPE: Chile. Dept. Linares: in the An-

des, (fr), *Germain s.n.* (holotype, herbarium not known, not seen).

*Cryptocarya nitida* Phil., *Linnaea* 33: 228. 1864–1865. TYPE: Chile. Santiago: at the foot of the Andes, Nov. 1862 (fl), *Philippi s.n.* (W, fide Kostermans, not seen).

*Bellota pauciflora* Phil., *Anales Univ. Chile* 26: 649. 1865. TYPE: Chile. Cordillera de Linares, Jan. (fl), *Germain s.n.* (SGO not seen).

Tree, height unknown. Terminal buds pubescent with appressed to ascending, straight hairs. Twigs terete, slightly compressed when young, densely or rarely sparsely pubescent with appressed to slightly ascending, short straight hairs, less densely when older. Leaves opposite; petioles 0.2–0.5(–0.8) cm long, flat to slightly canaliculate above, pubescent with appressed hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish ovate, 3–6  $\times$  2–4 cm; base round, not inrolled, apex obtuse to retuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 3 to 7 (9) pairs, almost immersed or slightly raised above, slightly raised below, tertiary veins not percurrent, minor venation pattern very coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed or slightly raised on both sides. Inflorescences in axils of leaves, sometimes on short branchlets (with or without leaves), racemose, rarely paniculate, 0.5–2 cm long, pubescent with erect hairs, rarely only sparsely pubescent, with 3 to 10 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers 2.5–3 mm long, 3–3.7 mm diam.; tepals 6, equal, almost round, 1.5–2 mm long, 1.3–1.8 mm wide, glabrous outside, sparsely to densely pubescent with almost appressed hairs at the base inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of innermost three stamens globose, 0.3–0.5 mm long; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.9 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Mature fruits unknown.

*Flowering time.* November and May.

*Distribution and habitat.* Central Chile (Fig. 7); reported to grow in subtropical, semiarid vegetation (Heusser, 1971).

*Common name.* Ulmo (*Bertero s.n.*).

*Selected specimens examined.* CHILE. **Bío-bío:** Concepción, 1855 (fl), *Germain s.n.* (BM, F, K). **Maule:** Cor-



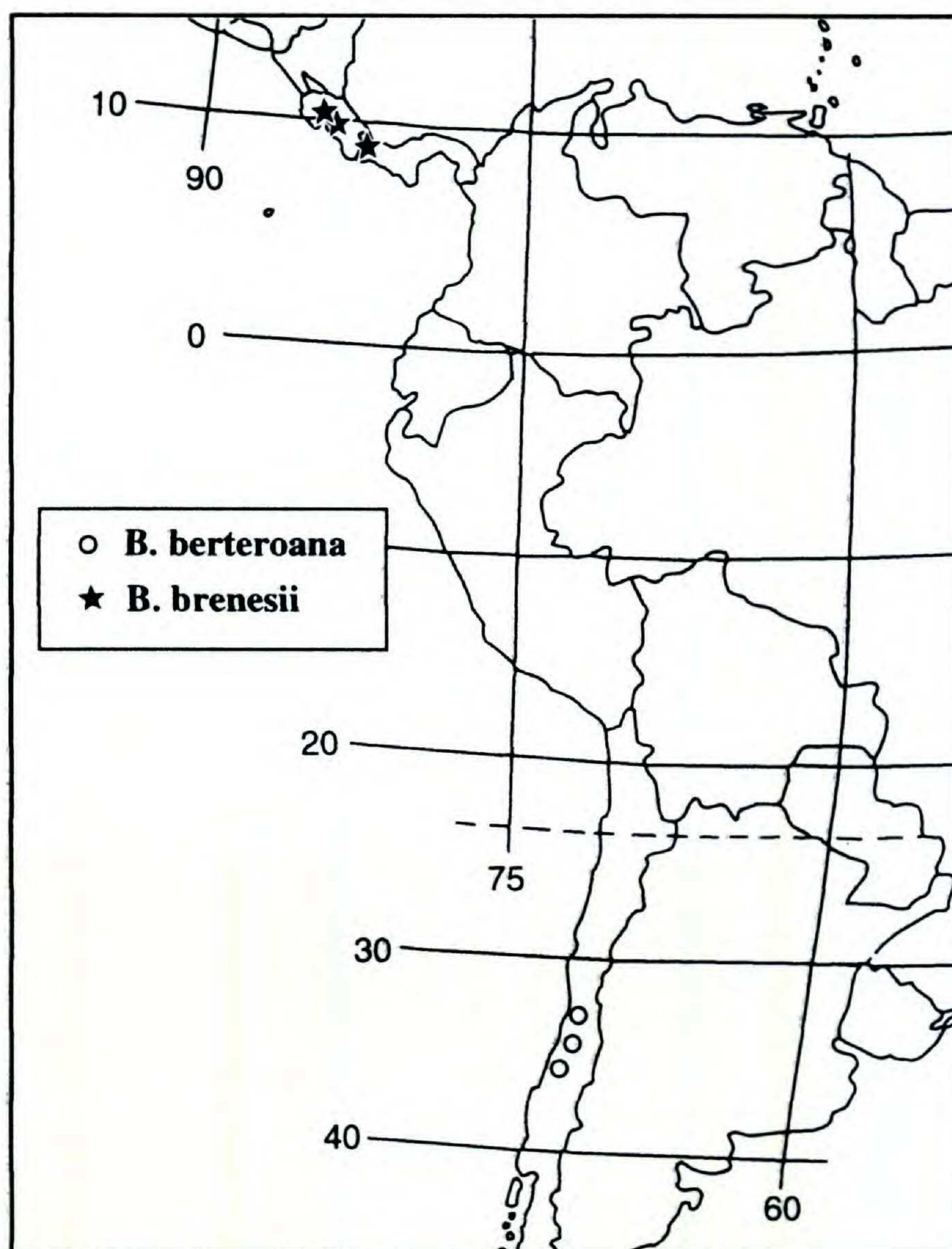


Figure 7. Representative distribution of *Beilschmiedia berteroana* and *B. brenesii*.

dillera de Linares, (fl), *Philippi 906* (K). **Valparaiso?**: Mt. la Leona, 1836 (fl), *Bertero 4* (BM).

Kostermans (1938: 859) recognized one of Bertero's collections in P as the lectotype of this species and stated, "Though Gay (*Flora Chilena* V, page 301) indicated no type specimen of his *Cryptocarya berteroana* it is evident that he described the specimens collected by Bertero (n. 4), as he cites the vernacular name: Ulmo and the name: *Adenostemum nitidum* Bertero, both names figuring on the labels of these specimens." I agree with Kostermans's designation, but the collection is not *Bertero 4* as he mentioned, but rather *Bertero s.n.* The specimen with a label saying "*Bertero 4*" is not in P but in BM. The label of this BM specimen does not include the vernacular name or the name *Adenostemum nitidum*. On the other hand, the Bertero specimen at P includes both of these names but without the numeral "4." Instead, the P label has the planetary symbol meaning "perennial." I suspect that Kostermans misread this planetary symbol as a "4." Since the BM and P

collections appear to be taken from different trees, I would like to clarify that the lectotype of this species is not "*Bertero 4*" as present in BM, but "*Bertero s.n.*" as in P.

I have not seen the types of *Bellota nitida*, *Cryptocarya nitida*, or *Bellota pauciflora*, but based on the descriptions of these species, it is clear to me that these taxa are conspecific with *Beilschmiedia berteroana*.

*Beilschmiedia berteroana* is one of the two species from Chile, with *B. miersii* being the other. These two Chilean species are unique among neotropical *Beilschmiedia* species in their opposite, roundish ovate leaves drying to light green and with a very coarse venation pattern. These Chilean species appear similar to one another at first glance, especially in leaf shape and venation pattern. However, *B. berteroana* has appressed or ascending, straight hairs on the terminal buds and twigs and has tepals glabrous outside. *Beilschmiedia miersii* has erect, curly hairs on the terminal buds and twigs and has tepals densely pubescent outside.



Cuticular characters also distinguish these two Chilean taxa (see Table 2).

It is interesting that *Cryptocarya alba* (Molina) Looser, also endemic to central Chile, shares vegetative macromorphological characters for leaves with these two Chilean species, but a quite different venation pattern and cuticular characters distinguish *Cryptocarya alba*. The similarity of all three Chilean species might be due to their xeric adaptations.

**6. *Beilschmiedia brenesii*** C. K. Allen, J. Arnold Arbor. 26: 415. 1945. TYPE: Costa Rica. Alajuela: La Palma and El Socorro de San Ramón, 24 July 1928 (fr), *Brenes 6214* (holotype, F!; isotype, NY!).

Tree, to 20(–35) m tall. Terminal buds pubescent with ascending or appressed, straight hairs, or almost glabrous. Twigs terete, compressed when young, glabrous, rarely pubescent with ascending straight hairs. Leaves opposite, relatively clustered near the terminal buds; petioles 0.5–0.8 cm long, flat or canaliculate, slightly thickened at the base, glabrous, concolorous with twigs; blades coriaceous, elliptic, (4–)6–9(–12) × 1.7–4.2(–6) cm; base cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 7 to 13 pairs, slightly or conspicuously raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed above, slightly or conspicuously raised below. Inflorescences usually clustered around terminal buds or on short leafless shoots, rarely in axils of leaves, paniculate, 3–9 cm long, sparsely pubescent with erect hairs to glabrous, with 20 to 50 flowers per inflorescence; floral pedicels of the lateral divisions (1.5–)3–5 mm long, pedicels of the central flowers up to 7 mm long. Flowers greenish yellow to creamy, 2.5–4 mm long, 2.6–3.2 mm diam.; tepals 6, equal, ovate, 1.3–2.2 mm long, 1–1.8 mm wide, almost glabrous or sparsely pubescent with ± appressed hairs outside, sparsely pubescent with appressed to erect (wavy) hairs inside; stamens 9, outer six filaments 0.4–0.6 mm long, innermost three stamens 0.5–0.8 mm long, filaments pubescent, anthers 0.7–1.1 mm long, 2-celled, anther apices obtuse to acute and glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pu-

bescent with appressed or rarely erect hairs, less densely toward the bottom. Fruits ellipsoid, black-purple, ca. 3.3 × ca. 1.8 cm, surface smooth; infructescence axis 2.5–3 mm diam., fruit pedicels thickened to 5 mm diam. below the fruit, but not constricted.

*Flowering time.* December to February.

*Distribution and habitat.* Costa Rica and western Panama (Fig. 7); (520–)900–1400(–1800) m; lower montane wet forest.

*Common names.* Chanco blanco (*Guindon & Brenes 35*), Chanco colorado (*Haber & Bello 4322*), Chanco rosado (*Haber & Bello 8434*) (Costa Rica).

*Selected specimens examined.* COSTA RICA. **Alajuela:** Cantón Alfaro Ruiz, 1700 m, 10 May 1941 (fr), *A. Smith 2717* (F). **Guanacaste:** Cantón de Liberia, Parque Nacional Guanacaste, Estación Cacao, 10°55'45"N, 85°28'15"W, 1100 m, 3 Oct. 1990 (fr), *Chávez 216* (CR, INB, MO). **Puntarenas:** Reserva Biológica Monteverde, Río Veracruz, 10°16'N, 84°22'W, 1300 m, 4 May 1991 (fr), *Bello et al. 2779* (INB, MO). PANAMA. **Chiriquí:** ca. 13 km from Río Sereno, Finca Hartmann, 8°50'N, 82°45'W, 1400–1800 m, 12 May 1991 (fr), *McPherson 15312* (MO).

*Beilschmiedia brenesii* belongs to the *B. hondurensis* group, with its closest species being *B. hondurensis* (see the discussion under *B. hondurensis*).

**7. *Beilschmiedia costaricensis*** (Mez & Pittier) C. K. Allen, J. Arnold Arbor. 26: 415. 1945. *Hufelandia costaricensis* Mez & Pittier, Bull. Herb. Boiss. II, 3: 228. 1903 (excl. *Pittier 1863* fide Kostermans). TYPE: Costa Rica. San José: forests of El Copey, 1800 m, Feb. 1898 (fl), *Tonduz 11713* (lectotype, designated by Kostermans (1938), B not seen; isolectotypes, BM!, CR!, G-BOIS not seen, K!, P!, US!).

*Beilschmiedia rohliana* Lasser, Bol. Acad. Cienc. Fis. Mat. y Nat. Caracas 10: 193. 1946. TYPE: Venezuela. Aragua: Henri Pittier National Park, a village of Rancho Grande, 14 Feb. 1946 (old fl & immature fr), *Lasser 2052* (holotype, VEN!).

*Cryptocarya kostermansiana* C. K. Allen, J. Arnold Arbor. 26: 423. 1945. TYPE: Costa Rica. Alajuela: Canton Naranjo, Naranjo, Cerro del Espiritu Santo, 1150 m, 24 Feb. 1940 (fl), *A. Smith P2418* (holotype, A photo!; isotypes, F!, US!).

Tree, to 30 m tall. Terminal buds pubescent with appressed to ascending, straight hairs. Twigs terete, compressed to angular when young, densely to sparsely pubescent with appressed to ascending, straight hairs, less densely pubescent when old. Leaves alternate; petioles 0.5–2 cm long, flat to canaliculate above, almost glabrous or pubescent



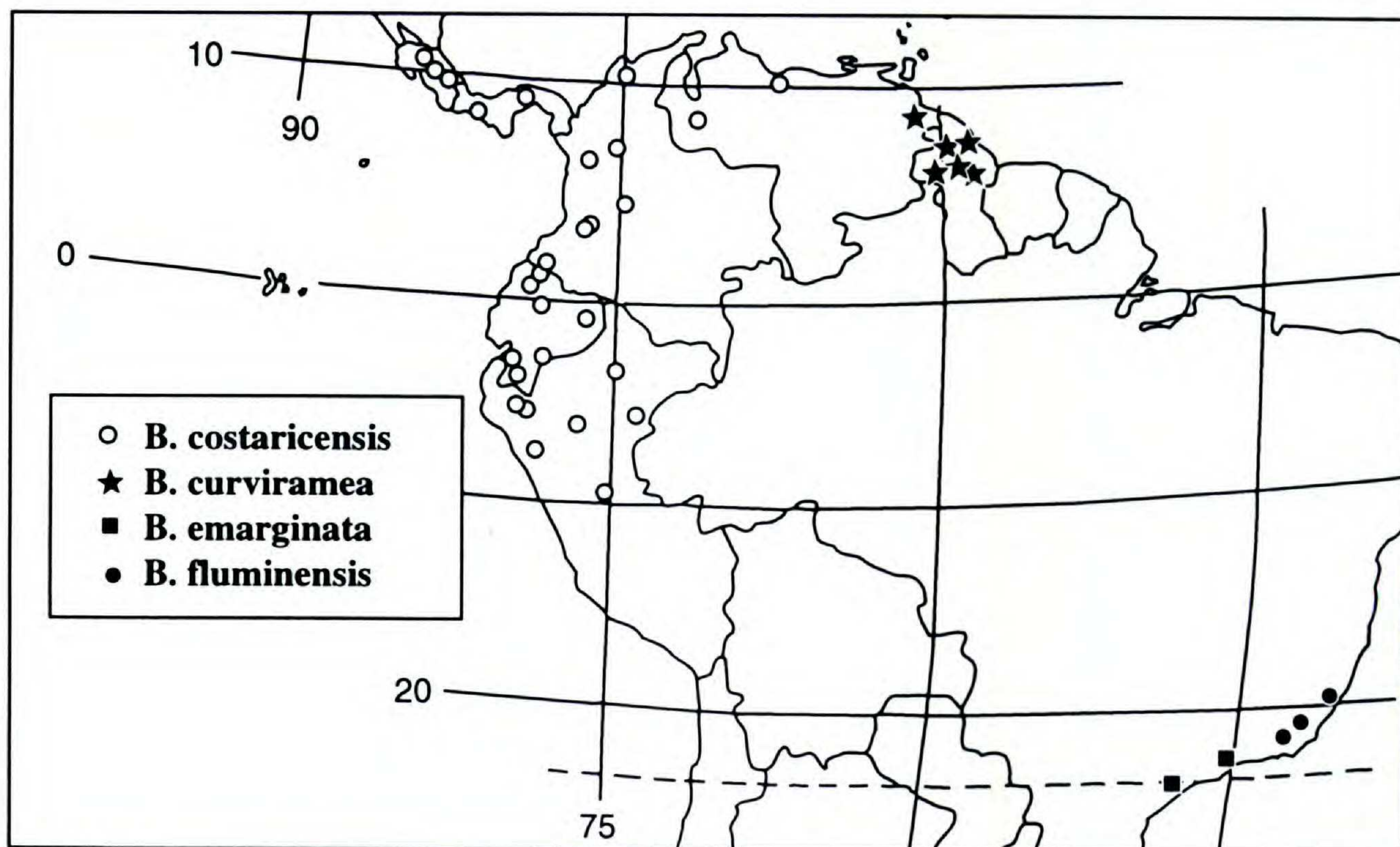


Figure 8. Representative distribution of *Beilschmiedia costaricensis*, *B. curviramea*, *B. emarginata*, and *B. fluminensis*.

with appressed to ascending hairs, concolorous with twigs; blades chartaceous to coriaceous, elliptic, 5–20(–26) × 2.5–9(–14) cm; base cuneate, not inrolled (rarely not only the base but the entire margin slightly inrolled), apex acute to acuminate, rarely obtuse; leaf surface glabrous on both sides or rarely lower leaf surface sparsely pubescent with appressed to ascending hairs, lower leaf surface not glaucous; midrib almost immersed above, raised below, secondary veins 5 to 11 (13) pairs, immersed above, raised below, tertiary veins ± percurrent, minor venation pattern fine to intermediate in size, areoles with branched free-ending veinlets inside, tertiaries and minor veins conspicuously to slightly raised on both sides. Inflorescences in axils of leaves, paniculate, 1–14(–16) cm long, sparsely pubescent with erect hairs, with (10) 25 to 50 (80) flowers per inflorescence; floral pedicels of the lateral divisions (0.3–)0.7–1.5 mm long, pedicels of the central flowers up to 4 mm long. Flowers creamy to whitish, 2–3 mm long, 2.3–2.8 mm diam.; tepals 6, equal, ovate, 1.3–1.8 mm long, 1–1.4 mm wide, pubescent with ± erect hairs on both sides; stamens 9, filaments 0.3–0.6 mm long, pubescent, anthers 0.6–0.9 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.1–1.8 mm long, glabrous to sparsely pubescent, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely pu-

bescent toward the bottom. Fruits ellipsoid, purple-black, 3–4(–5) × 1.5–2(–3) cm, surface smooth; infructescence axis 1.5–3.5 mm diam., fruit pedicels slightly thickened to 5 mm diam. below the fruit, but not apically constricted.

*Flowering time.* Usually January through May.

*Distribution and habitat.* Costa Rica, Panama, western Venezuela, western Colombia, Ecuador, and northern Peru (Fig. 8); (100)750–2300(3000) m; premontane wet forest to cloud forest.

*Common names.* Chanco (*Haber & Zuchowski 8746*) (Costa Rica); Aguacatillo (*Benalcazar & Silva 19*) (Colombia); Aguacatillo (*Poortmann s.n.*), Pacche (*Quelal & Tipaz 124*), Huevo cuguán/Malde (*Thomsen 58818*) (Ecuador); Palo oso (*Díaz & Baldeón 2464*), Puma (*Díaz 2088*), Pumapara (*Sagastegui et al. 12408*) (Peru).

*Selected specimens examined.* COSTA RICA. **Alajuela:** Reserva Biológica Monteverde, Río Peñas Blancas, 10°18'N, 84°45'W, 900 m, 1 Jan. 1987 (fl), *Haber & Bello 6531* (MO). **Cartago:** El Muñeco, on the Río Navarro, 1400–1500 m, 6–7 Mar. 1926 (immature fr), *Standley & Torres 51271* (US). **Guanacaste:** Chiripa, Tilarán, 4 km N of La Florida, 10°26'N, 84°54'W, 1100 m, 14 Jan. 1987 (fl), *Haber & Bello 6559* (MO). **Heredia:** Cantón Central, 11 km E of Cariblanco, 10°16'N, 84°05'W, 1060 m, 18 Apr. 1988 (young fl), *Loiselle 384* (CR). **Limón:** Cordillera de Talamanca, Fila Carbón, ca. 6 km W de Home Creek, 9°40'10"N, 82°50'35"W, 100 m, 14 Feb. 1991 (fl), *Hammel et al. 18116* (CR, F, MO). **Puntarenas:** Cantón de Coto Brus, Santa María de Pittier, 9°01'38"N, 82°51'56"W, 1700 m, 10 June 1995 (fr), *J. González 790* (INB). **San**



**José:** Sta. Ma de Dota-El Cedral, 12 June 1975 (sterile), *Poveda 1068* (CR, F). PANAMA. **Chiriquí:** Cerro Horqueta, 2100 m, 24 July 1966 (fl), *Blum & Dwyer 2624* (MO). **Panamá:** Cerro Azul, ca. 180 m, 17 July 1962 (immature fr), *Dwyer 2054* (MO). VENEZUELA. **Aragua:** Henri Pittier Parque Nacional, along road towards Rancho Grande, 1000–1200 m, 25 July 1994 (fl), *Lorea & Carnevali 5563* (MO). **Mérida:** La Chorrera, Carretera Mérida–Azulita, 3 Feb. 1987 (fl & fr), *van der Werff et al. 8786* (MO). COLOMBIA. **Antioquia:** Municipio Campamento, Vereda El Alto, 4 km W of mine “Las Brisas,” 1 km from gorge “El Niño,” 7°03'N, 75°19'W, 1810 m, 9 Sep. 1989 (fl), *Callejas et al. 8368* (MO). **Cundinamarca:** Laguna Pedro Palo above Finca San Jose, ca. 32 km Mosquera-La Mesa, 2000–2250 m, 1 Aug. 1976 (immature fr), *Gentry & Fallen 17136* (MO, NY). **Valle:** Peñas Blancas, cuenca río Pichindé, 1800 m, 11 June 1977 (young fl), *Benalcazar & Silva 19* (MO). **Magdalena:** Sierra de Perijá, E of Manaure, Hacienda Nuevo Horizonte, El Podrido, 1550–1600 m, 16 Nov. 1959 (immature fr), *Cuatrecasas & Romero-Castaneda 25413* (US). **Nariño:** 7 km from Chucunés, Planada Natural Reserve, 1°10'N, 77°58'W, 1800 m, 16 Nov. 1987 (fl), *de Benavides 8964* (MO). EC-UADOR. **Carchi:** Gualpí Alto area, 01°02'N, 78°23'W, 900–1000 m, 18–25 May 1985 (immature fr), *Thomsen 58818* (MO). **El Oro:** Los Puntos de Guarumal, 1875 (immature fr), *Poortmann s.n.* (P). **Imbabura:** Road Otavalo–Apuela, 2000–3000 m, 14 Feb. 1989 (fl & immature fr), *van der Werff & Palacios 10574* (MO). **Loja:** El Colorado to 5 km NE of Alamor, 3°59'S, 79°58'W, 1200 m, 10 Aug. 1975 (immature fr), *Samaniego & Vivar 79* (US). **Morona-Santiago:** Bomboiza, Misión Salesiana-Shuar and around there, 03°25'S, 78°35'W, 800 m, 8–10 June 1986 (fl & fr), *Zaruma & Arguello 485* (MO). **Napo:** Aguarico, Reserva Etnica Huaorani, 245 m, 9 Mar. 1995 (immature fr), *Aulestia 3494* (MO). **Pichincha:** along new road Nanegal–Mindó, 1600–2500 m, 1 Mar. 1994 (fl & fr), *van der Werff et al. 13368* (MO). PERU. **Cajamarca:** Cutervo National Park, 12 km NE of San Andres de Cutervo, 06°10'S, 78°40'W, 2230 m, 11 Sep. 1991 (sterile), *Gentry et al. 74662* (MO). **Loreto:** C. I. Jenaro Herrera, Trocha Arboretum Braga, Tahuampa forest, 04°55'S, 73°45'W, 120–125 m, 29 Sep. 1991 (fr), *Grandez & Koor 2883* (MO). **Huánuco:** Prov. Puerto Inca, Dpto. Yuyapichis, 09°40'S, 75°02'W, 270 m, 1–15 Nov. 1990 (fr), *Tello 590* (MO). **Piura:** Huancabamba, Distrito Canchaque, Chorro Blanco, 1500–1900 m, 18 Apr. 1987 (immature fr), *Díaz & Baldeón 2464* (MO). **San Martín:** Rioja Province, Carretera Rioja–Pedro Ruiz, Caves of Aguas Verdes, 950 m, 24 Mar. 1998 (fl), *van der Werff et al. 15585* (MO).

This species is distinguished by the following characters: appressed to ascending hairs on the terminal buds and young twigs, alternate leaves, areoles with branched free-ending veinlets, non-glaucous lower leaf surfaces, glabrous anthers, and fruit pedicels not constricted at the apices. This is sometimes misidentified as *B. pendula* due to its similar pubescence type, leaf shape, flower structure, and fruit shape (see the discussion under *B. pendula*).

Many Colombian and Ecuadorian collections for *Beilschmiedia costaricensis* appear different from collections from other countries (and some collec-

tions from Colombia) by their coriaceous leaves, coarser and less raised venation pattern, and sparsely pubescent pistils. Additionally, these collections tend to have shorter petioles and larger leaves. However, differences of the leaf texture and venation pattern between them are subtle, and it is difficult to make a clear separation: petiole lengths and leaf sizes show no clear distinction. Pubescence on pistils in the former collections cannot be used to distinguish these collections because this pistil indumentum is very sparse and easily missed. Separating these collections as a new species would only create confusion, so they are best placed within *B. costaricensis*.

**8. *Beilschmiedia curviramea* (Meisn.) Kosterm.,** *Rec. Trav. Bot. Néerl.* 35: 853. 1938. *Aydendron curvirameum* Meisn., in DC., *Prodr.* 15(1): 90. 1864. *Hufelandia curviramea* (Meisn.) Mez, *Jahrb. Königl. Bot. Gart. Berl.* 5: 19. 1889. SYNTYPES: Guyana. Roraima, 1842–1843 (fl), *Schomburgk 1009* (B photo!, BM!, BR not seen, G-BOIS not seen, G-DEL not seen, LZ not seen, NY not seen, P!, W not seen); Demerara, Apr. 1844 (fl), *Schomburgk 1730* (K!).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, almost glabrous or sparsely pubescent with appressed hairs. Leaves opposite, rarely subopposite; petioles 0.6–1.5(–2.2) cm long, flat or canaliculate above, glabrous, slightly discolored or rarely concolorous with twigs; blades coriaceous, elliptic, (6–)9–20 × (2.5–)4–6.5(–8.5) cm; base cuneate to obtuse, not inrolled, apex acute or rarely cuspidate; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 8 to 13 (16) pairs, slightly raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed above, slightly raised or almost immersed below. Inflorescences in axils of leaves, very rarely clustered on a leafless short shoot, paniculate with few branches, 3–7(–12.5) cm long, sparsely pubescent with erect hairs, with 20 to 30 (50) flowers per inflorescence; floral pedicels of the lateral divisions 1–3 mm long, pedicels of the central flowers up to 5 mm long. Flowers yellow to white, ca. 2 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate to elliptic, 1.5–2 mm long, 1.2–1.7 mm wide, sparsely pubescent with ± appressed hairs outside, almost glabrous inside; stamens 9, outer six filaments 0.3–0.4 mm long, innermost



three filaments 0.4–0.6 mm long, filaments pubescent, anthers 0.8–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs or glabrous. Fruits ellipsoid, black, 3–5 × 2–4 cm, surface smooth or rarely slightly warty; infructescence axis ca. 2.5 mm diam., fruit pedicels thickened to 4–5 mm diam. below the fruit and not constricted.

*Flowering time.* February, April to July, September to November.

*Distribution.* Eastern Venezuela and northern Guyana (Fig. 8); 0–650 m.

*Common names.* Aguacatillo moises (*Marcano-Berti* 387) (Venezuela); Lana-balli (*Persaud* 70) (Guyana).

*Selected specimens examined.* VENEZUELA. **Bolívar:** E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 km N of Tumeremo, vicinity of Deborah, Nuria Plateau, 600–650 m, 5–8 Feb. 1961 (fl & fr), *Steyermark* 89161 (F, NY). **Amacuro:** E of Rio Grande, NE of El Palmar, near the border of Estado Bolívar, 19 Aug.–7 Sep. 1964 (immature fr), *Marcano-Berti* 387 (F, MO, NY). GUYANA. **Cuyuni-Mazaruni:** W bank of Essequibo River 0–2 km S of Wolga settlement, 06°27'N, 58°38'W, 0–15 m, 24 Dec. 1992 (fl), *Henkel* 650 (MO). **Upper Demerara-Berbice:** between the Demerara and Berbice Rivers, ca. 5°50'N, 15–19 July 1922 (fl), *de la Cruz* 1655 (F, MO, NY).

Kostermans (1938) apparently regarded *Schomburgk* 1009 and 1730 as identical. However, *Schomburgk* 1009 was collected in 1842–1843, and *Schomburgk* 1730 in April 1844.

*Beilschmiedia curviramea* is the only member of the *B. curviramea* group found outside southeastern Brazil. This species shares similar leaf and flower structures with *B. stricta*, but tends to have larger leaves, less conspicuously raised blade venation, and less pubescent flowers than seen in *B. stricta*. It is uncertain whether these characters consistently distinguish these two species since only one collection was examined for *B. stricta*.

Beyond the *Beilschmiedia curviramea* group, *B. curviramea* appears to be vegetatively similar to the Costa Rican species, *B. brenesii*, but leaves of *B. brenesii* cluster nearer the tips of branches and have a blade venation pattern conspicuously raised below. Leaves of *B. curviramea* are evenly distributed along the twigs and have a venation pattern almost immersed on both sides.

**9. *Beilschmiedia emarginata* (Meisn.) Kosterm.,** Rec. Trav. Bot. Néerl. 35: 855. 1938. *Cryptocarya emarginata* Meisn., in DC., Prodr. 15(1): 76. 1864. *Hufelandia emarginata* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 18. 1889. TYPE: Brazil. São Paulo: near Lorena, Oct. 1833 (fl), *Riedel* 1585 (holotype, LE!; isotypes, G-BOIS not seen, K!, NY not seen).

Tree, to 15 m tall. Terminal buds pubescent with ferruginous erect, short curly hairs. Twigs terete, compressed when young, sparsely pubescent with short erect curly hairs or almost glabrous. Leaves opposite; petioles ca. 0.5 cm long, flat above, sparsely pubescent or glabrous, concolorous with or slightly darker than twigs; blades chartaceous, elliptic, often asymmetrical and sinuate, 6.5–12 × 3–6.5 cm; base cuneate, not inrolled, apex emarginate to rounded; leaf surface glabrous on both sides; uncertain whether lower leaf surface glaucous or not; midrib immersed above, raised below, secondary veins 7 or 8 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, slightly raised or almost immersed above, slightly raised below. Inflorescences in axils of leaves, paniculate, 3–5 cm long, almost glabrous or sparsely pubescent with short erect curly hairs, with 15 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2–2.8 mm long, 2.2–2.8 mm diam.; tepals 6, equal, ovate, 1.2–1.5 mm long, 0.8–1.2 mm wide, almost glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, outer six anthers ca. 0.9 mm long, innermost three anthers ca. 0.7 mm long, all the anthers 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1–1.5 mm long, glabrous, ovary as long as pistil and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits unknown.

*Flowering time.* October and December.

*Distribution.* São Paulo, Brazil (Fig. 8).

*Additional specimen examined.* BRAZIL. **São Paulo:** Botanical Garden (native), 9 Dec. 1955 (sterile), *Kuhlmann* 3885 (NY).

Among southeastern Brazilian *Beilschmiedia* species, *B. emarginata* is distinguished by its ferruginous, short, and erect pubescence on terminal



buds and twigs. Additionally, this species usually has undulate leaves and emarginate leaf apices, features not seen in the other southeastern Brazilian species.

**10. *Beilschmiedia fluminensis*** Kosterm., Rec. Trav. Bot. Néerl. 35: 865. 1938. TYPE: Brazil. Rio de Janeiro: Estado Rio G. Portella, Monte Sinai, 1935 (fl), *Nunes 323* (holotype, U not seen; isotype, RB!).

Tree, to 15 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly compressed when young, almost glabrous or sparsely pubescent with appressed hairs. Leaves opposite; petioles 1–2 cm long, canaliculate above, glabrous, slightly darker than twigs; blades firmly chartaceous, elliptic, (10–)13–16(–18) × 4–7 cm; base cuneate, slightly inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides, rarely lower leaf surface sparsely pubescent with short appressed hairs; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 12 to 14 pairs, raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised above, raised below. Inflorescences in axils of leaves, paniculate, 4–7 cm long, glabrous to sparsely pubescent with erect hairs, with 20 to 35 flowers per inflorescence; floral pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 2.5 mm long. Flowers greenish, 1.7–2 mm long, 2–2.5 mm diam.; tepals 6, equal, elliptic to ovate, 1–1.5 mm long, 1.1–1.5 mm wide, glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, filaments pubescent, anthers 0.7–0.9 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs around the base of stamens and staminodia. Fruits ellipsoid, 4.5–5 × ca. 3 cm, the surface warty or smooth; fruit pedicels ca. 2.5 mm diam., thickened to ca. 4 mm diam., not apically constricted.

*Flowering time.* September and October.

*Distribution.* Rio de Janeiro and Espírito Santo, Brazil (Fig. 8).

*Selected specimens examined.* BRAZIL. **Rio de Janeiro:** Malo Breuro, 25 Oct. 1927 (fl), *Auleuis s.n.* (RB).

**Espírito Santo:** margin of Rio Paucos, road of Colomia, Colatina, 2 May 1934 (fr), *Kuhlmann 292* (RB).

Collections of *Beilschmiedia fluminensis* have sometimes been misidentified as *B. taubertiana* or *B. emarginata*. *Beilschmiedia fluminensis* can be distinguished from the two species by its appressed pubescence on terminal buds and twigs. *Beilschmiedia taubertiana* has erect, long pubescence while *B. emarginata* has erect, short curly pubescence. Further, petioles of *B. fluminensis* are relatively longer than the other two species. The species most similar to *B. fluminensis* is *B. stricta*, which shares a similar indument type, leaf shape, and flower structure. Differences between *B. fluminensis* and *B. stricta* are leaf bases (slightly inrolled vs. flat) and inflorescences (paniculate and almost glabrous vs. racemose and relatively densely pubescent).

**11. *Beilschmiedia hexanthera*** van der Werff, Brittonia 47: 374. 1995. TYPE: French Guiana. Vicinity of Eau Claire: near Saül, 200 m, 9–10 Aug. 1993 (fl), *van der Werff et al. 12951* (holotype, MO!; isotypes, CAY not seen, NY not seen).

Tree, to 20 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, ± densely pubescent with short appressed hairs, less densely pubescent to glabrescent when old. Leaves alternate; petioles 0.6–1.3 cm long, flat to canaliculate, sparsely pubescent with short appressed hairs, concolorous with twigs; blades firmly chartaceous, elliptic, (5.5–)8–12(–16) × (2.5–)4–6 cm; base cuneate, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface pubescent with short appressed hairs; lower leaf surface not glaucous; midrib immersed or slightly raised above, raised below, secondary veins (5) 7 to 9 pairs, almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins almost immersed on both sides (the pattern visible on both sides, coarser on the upper surface than on the lower). Inflorescences in axils of leaves, paniculate, (3–)6–11 cm long, sparsely pubescent with short erect hairs, with 25 to 50 (75) flowers per inflorescence; floral pedicels of the lateral divisions 0.3–0.5 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers greenish yellow, ca. 1.5 mm long, 1.7–2.1 mm diam.; tepals 6, equal, broadly ovate, 0.5–0.8 mm long, 0.6–1 mm wide, sparsely pubescent with short erect hairs outside, sparsely pubescent with appressed hairs inside, or with erect curly hairs at the



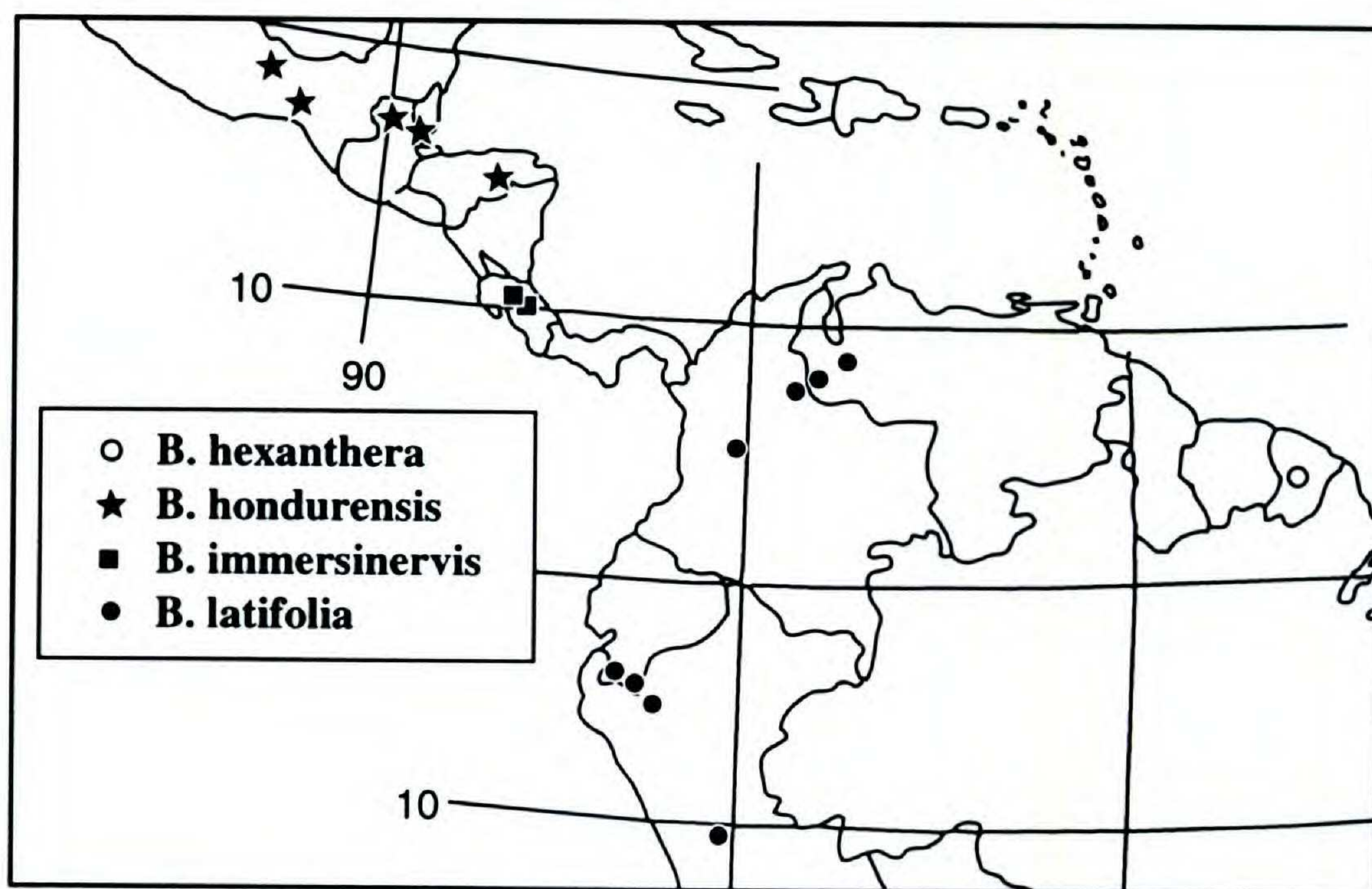


Figure 9. Representative distribution of *Beilschmiedia hexanthera*, *B. hondurensis*, *B. immersinervis*, and *B. latifolia*.

base inside; stamens 6, representing the outer two whorls, filaments ca. 0.2 mm long, pubescent, anthers ca. 0.4 mm long, 2-celled, anther apices obtuse to truncate and glabrous; staminodia 6, the three staminodia representing the third whorl subulate, 0.5–0.7 mm long, the lower half pubescent, glands on the three staminodia globose to reniform; the three staminodia representing the fourth whorl deltoid, ca. 0.5 mm long; pistil 1–1.2 mm long, glabrous, ovary  $\pm$  as long as and gradually narrowed into the style; receptacle pubescent with erect curly hairs (upper part of the receptacle) and long appressed hairs (lower part of the receptacle). Fruits unknown.

*Flowering time.* August.

*Distribution and habitat.* French Guiana (Fig. 9); 200–400 m; unflooded forest.

*Additional specimen examined.* FRENCH GUIANA. **Saint-Laurent-du-Maroni:** Saül and vicinity, Route of Bélizon, S of Eaux Claires, 3°37'N, 53°12'W, ca. 200–400 m, 21 Aug. 1993 (fl), *Mori et al.* 23377 (MO).

*Beilschmiedia hexanthera* is the only neotropical *Beilschmiedia* species with only six fertile stamens. According to Hyland (1989) there are several *Beilschmiedia* species with six fertile stamens in Australia, but as van der Werff (1995) suggested, it is unlikely that *B. hexanthera* and the Australian species are closely related. This reduction in stamen number probably occurred independently in French Guiana and Australia. *Beilschmiedia hexanthera* shares with *B. pendula* similar vegetative and floral characters (except for the stamens in the third whorl). However, *B. hexanthera* does not have the glaucous leaves of *B. pendula*.

**12. *Beilschmiedia hondurensis*** Kosterm., Rec. Trav. Bot. Néerl. 35: 854. 1938. TYPE: Belize: Camp 31, British Honduras-Guatemala Survey, 630 m, 7 Apr. 1934 (fr), *Schipp* 1262 (holotype, K not seen; isotypes, AFS not seen, BM!, G-DEL not seen, F!, K!, NY!).

Tree, to 30 m tall. Terminal buds pubescent with appressed or slightly ascending, straight hairs. Twigs terete, compressed when young, glabrous. Leaves opposite; petioles 0.5–1(–1.2) cm, flat or canaliculate above, glabrous, darker than or concolorous with twigs; blades firmly chartaceous, elliptic, (5–)8.3–13.2(–18)  $\times$  (1.5–)2.9–4.6(–6.5) cm; base cuneate, not inrolled, apex acuminate, rarely acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins (7) 9 to 12 (14) pairs, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets, tertiaries and minor veins slightly raised above, raised below. Inflorescences in axils of leaves or around terminal buds, paniculate with few branches, 3–6 cm long, sparsely pubescent with appressed to erect hairs, sometimes almost glabrous, with 10 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.0 mm long, pedicels of the central flowers up to 2 mm long. Flowers ca. 3 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate, 1.5–2.1 mm long, 1.3–1.5 mm wide, sparsely pubescent with  $\pm$  appressed hairs outside, sparsely pubescent with relatively long appressed to erect hairs inside, sometimes almost glabrous in-



side; stamens 9, filaments ca. 0.5 mm long, sparsely pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices acute or rarely obtuse, anther apices glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.5 mm long; pistil ca. 1.3 mm long, glabrous, ovary as long as or longer than and gradually narrower into the style; receptacle sparsely pubescent with erect hairs, less densely toward the bottom. Fruits ellipsoid, black,  $2.3\text{--}3 \times$  ca. 1.3 cm (immature?), surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels slightly thickened to 3 mm diam. below the fruit, apically constricted or rarely not constricted.

*Flowering time.* February.

*Distribution and habitat.* Eastern Mexico, Belize, northern Guatemala, Honduras (Fig. 9); (200–)750–1600(–1850) m; from wet tropical forest to montane forest.

*Selected specimens examined.* MEXICO. **Chiapas:** Municipio of Cintalapa, SE of Cerro Baul on the border with the state of Oaxaca, 1600 m, 8 Jan. 1973 (immature fr), *Breedlove & A. R. Smith 31417* (MEXU, MO, NY). **Oaxaca:** Municipio San Miguel Chimalapa, Cerro Salomón, near the border with Municipio Sta. Maria Chimalapa,  $16^{\circ}45'N$ ,  $94^{\circ}11'30"W$ , 1850 m, 23 Dec. 1985 (immature fr), *Wendt et al. 5151* (MEXU, MO). **Veraacruz:** Municipio Sn. Andres Tuxtla, Laguna Escondida, 3 km N of station of Biología Tropical Los Tuxtlas, 200 m, 21 Feb. 1985 (fl), *Ibarra et al. 2292* (MEXU, MO). GUATEMALA. **Petén:** La Cumbre, 142/143 km E of the Cadenas Road, 11 May 1975 (young fl), *Lundell 19280* (MO). BELIZE. **Toledo:** SW of Mt. Maya, Columbia River Forest Reserve, Glorcia Camp,  $16^{\circ}22'N$ ,  $89^{\circ}10'W$ , 750 m, 13–14 Apr. 1992 (immature fr), *Holst 4435* (BM, MO). HONDURAS. **Olancho:** trail between La Chorrera campsite and 1900 m camp on ridge,  $14^{\circ}59'N$ ,  $88^{\circ}56'W$ , 1500 m, 31 May 1992 (fl), *Thomas 412* (MO).

The type collection of *Beilschmiedia hondurensis* is reported as a shrub, but some collections have been described as tall as 30 m.

Most closely related to *Beilschmiedia hondurensis* is *B. brenesii*. Some, if not all, Mexican collections placed in *B. hondurensis* approach *B. brenesii*, making the distinction between the two species difficult. *Beilschmiedia hondurensis* is usually distinguished from *B. brenesii* by its petioles darker than twigs, shorter floral pedicels, and fruit pedicels apically constricted. However, Mexican collections have the petioles concolorous with twigs and fruit pedicels not constricted at the apices. Typical *B. hondurensis* specimens have acuminate leaf apices, but these Mexican collections sometimes have acute leaf apices and are similar to most *B. brenesii*.

For reproductive characters, *Beilschmiedia hondurensis* differs from *B. brenesii* by its shorter floral pedicels. However, only one collection in *B. hondurensis* reveals flowers in good condition, and it is

from an unusually low elevation for *B. hondurensis* (even for *B. brenesii*). More fertile material of *B. hondurensis* is clearly needed to distinguish *B. hondurensis* from *B. brenesii*.

**13. *Beilschmiedia immersinervis*** Sa. Nishida, sp. nov. TYPE: Costa Rica. Guanacaste: Cantón de Abangares, Cordillera de Tilarán, de Santa Elena hacia San Rafael, Zona Monteverde,  $10^{\circ}20'00"N$ ,  $84^{\circ}53'00"W$ , 1200 m, 7 Jan. 1992 (fl & fr), *Guindon & Brenes 36* (holotype, MO!; isotype, INB!). Figure 10.

Haec species habitu *Beilschmiediae pendulae* similis, sed ab ea trichomatibus erectis atque antheris pubescentibus, ab aliis speciebus neotropiceis nervis in hypophyllo immersis differt.

Tree, to 30 m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, compressed or sulcate when young, densely to sparsely pubescent with erect curly hairs, less densely pubescent to almost glabrous when older. Leaves alternate to subopposite, rather clustered near the terminal buds; petioles 0.7–1.5 cm long, flat above, pubescent with erect curly hairs, concolorous with twigs; blades firmly chartaceous, oblanceolate to elliptic,  $6\text{--}10\text{--}13 \times 2\text{--}4\text{--}6$  cm; base attenuate to cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 7 to 10 pairs, immersed on both sides (visible on lower leaf surface), tertiary veins weakly percurrent, minor venation pattern fine, arcoles without free-ending veinlets inside, tertiaries and minor veins immersed and hardly visible above, almost immersed or very slightly raised below. Inflorescences in axil of the leaves near the terminal buds, paniculate with few branches, 2–6 cm long, pubescent with short erect hairs, with 10–30(–50) flowers per inflorescence; floral pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers greenish yellow, ca. 2.8 mm long, ca. 2.6 mm diam.; tepals 6, equal, elliptic to ovate, ca. 2.2 mm long, 1.3–1.7 mm wide, pubescent with erect or appressed hairs on both sides; stamens 9, outer six filaments ca. 0.6 mm long, innermost three filaments ca. 0.8 mm long, filaments pubescent, anthers ca. 0.8–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.3–1.8 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits ellipsoid, shiny black, ca.  $2.5 \times$  ca. 1.5 cm,



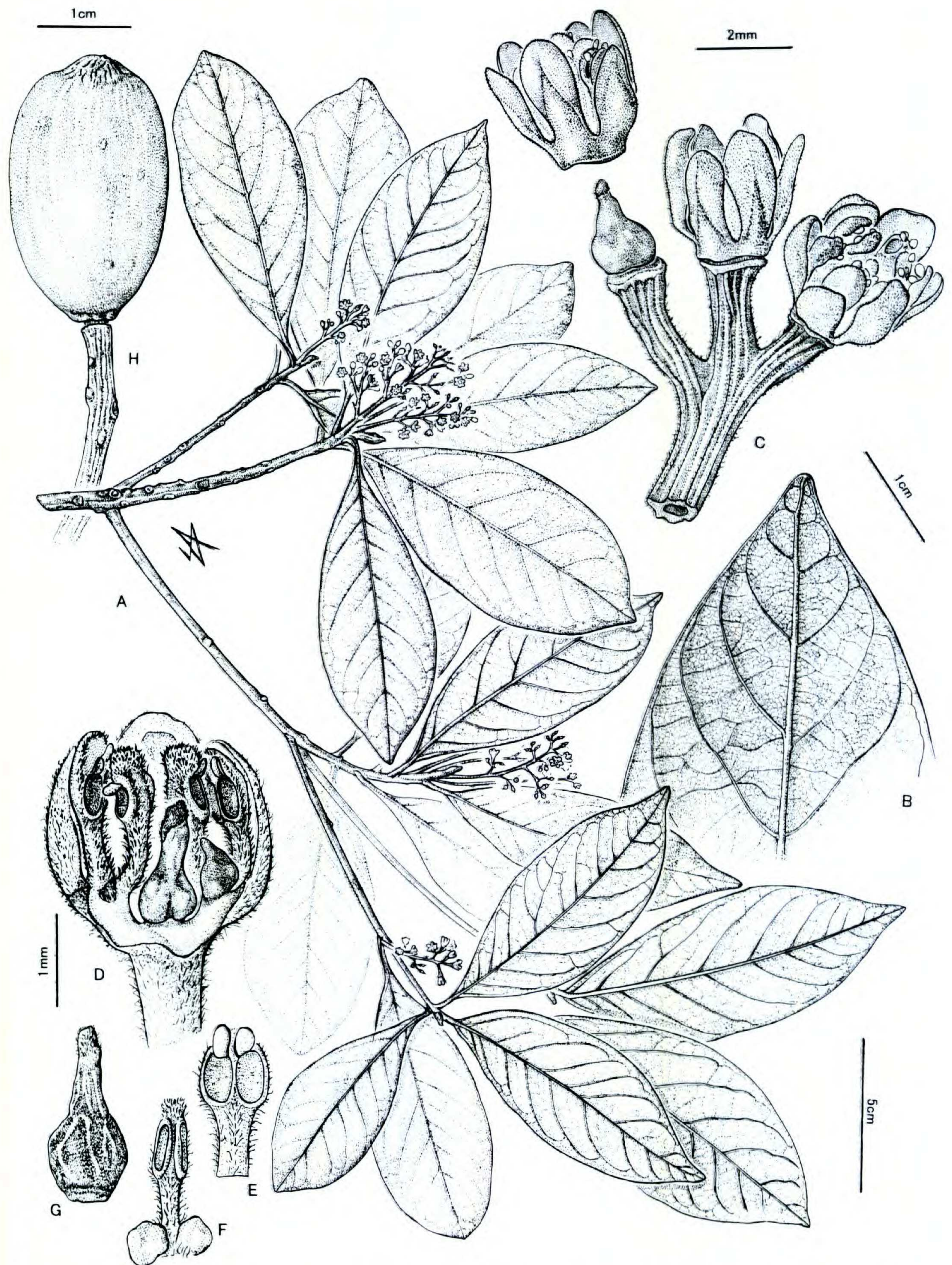


Figure 10. *Beilschmiedia immersinervis* (A–G, Guindon & Brenes 56; H, Haber 11070). —A. Flowering branch. —B. Detail of lower leaf surface. —C. Part of inflorescence with one flower in anthesis. —D. Flower with tepals removed, showing stamens, staminode, and pistil. —E. Stamen of whorl I/II, ventral view. —F. Stamen of whorl III with two glands, dorsal view. —G. Pistil. —H. Fruit.



surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels rarely slightly thickened to 3 mm diam., slightly constricted at the apices or almost not constricted.

*Flowering time.* December and January.

*Distribution and habitat.* Western Costa Rica (Fig. 9); 300–1400 m; premontane wet forest.

*Paratypes.* COSTA RICA. **Alajuela:** along a road between Canas and Upala, lower slopes Volcán Tenorio, 450 m, 23 Jan. 1984 (fl), *Pennington & Poveda 11416* (CR). **Guanacaste:** Parque Nacional Guanacaste, Estación Pitalilla, La Pasmompa, 11°02'N, 85°25.3'W, 300 m, 17 June 1989 (fr), *Hammel et al. 17502* (INB, MO); Cantón de Tilarán, San Rafael to El Dos de Tilarán, 10°22'N, 84°53'W, 800–1100 m, 11 Mar. 1992 (fr), *Haber et al. 11070* (INB, MO); same cantón, San Rafael de Abangares, 10°20'35"N, 84°53'25"W, 1060 m, 10 Mar. 1996 (fr), *Yasuda et al. 1312* (INB, MO); Los Tornos, 10°21'N, 84°51'W, 1300 m, 14 Apr. 1987 (fr), *Haber & Bello 6967* (F, INB, MO). **Puntarenas:** Cantón de Puntarenas, Cordillera de Tilarán, Santa Elena, near Cañitas, Zona Monteverde, 10°19'30"N, 84°49'30"W, 1400 m, 1 Dec. 1992 (fl), *Guindon & Brenes 56* (CR, INB, MO, USJ).

*Beilschmiedia immersinervis* is distinguished by the following four characters: short curly pubescence on the terminal buds and twigs, leaves alternate, secondary veins immersed on both sides of the leaves, and anther apices pubescent. Some collections of *B. immersinervis* have been identified as *B. pendula*, probably because its leaf shape is similar to that of *B. pendula*. However, *B. immersinervis* can be separated from *B. pendula* by its erect and curly hairs on the terminal buds and pubescent anther apices.

*Beilschmiedia immersinervis* shares pubescence type and venation pattern with *B. steyermarkii*. However, *B. immersinervis* has pubescent anther apices and firmly chartaceous, symmetrical leaves, while *B. steyermarkii* has glabrous anther apices and more typically coriaceous, asymmetrical leaves.

This species also shares a similar venation pattern and pubescent anthers with *B. riparia*, but *B. immersinervis* is distinguished from this species by its immersed secondary veins. *Beilschmiedia immersinervis* also differs in its smaller, oblanceolate, glaucous leaves and slightly longer floral pedicels.

**14. *Beilschmiedia latifolia*** (Nees) Sa. Nishida, comb. nov. Basionym: *Hufelandia latifolia* Nees, Syst. Laur.: 674. 1836. TYPE: Peru. Locality not indicated, 1835 (fl), *Matthew 1433* (holotype, E!; isotypes, BM!, E!, K!, LE not seen, OXF not seen).

Tree, to 25 m tall. Terminal buds densely pubescent with brown to ferruginous, erect, long,

wavy to straight hairs. Twigs terete, angular when young, densely pubescent with long erect hairs, less densely pubescent when older. Leaves alternate; petioles 0.5–1.5 cm long, flat above, pubescent with long erect hairs to glabrous, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, (5–)7–11(–18) × 4–8(–11.5) cm; base obtuse to rounded, not inrolled, apex obtuse; upper leaf surface glabrous, lower leaf surface densely pubescent with long hairs when young, less densely pubescent to rarely almost glabrous when old; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 6 to 9 pairs, immersed or impressed, rarely slightly raised above, raised below, tertiary veins usually percurrent, rarely only weakly percurrent, minor venation pattern fine, areoles lacking free-ending veinlets inside, tertiaries and minor veins immersed above, immersed (the pattern visible) or slightly raised below. Inflorescences in axils of leaves, paniculate, 6–11 cm long, densely pubescent with long erect hairs, with 20 to 40 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 mm long. Flowers 2.5–3 mm long, ca. 2.8 mm diam.; tepals 6, equal, ovate, 1.7–2.2 mm long, 1–1.5 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments ca. 0.3 mm long, innermost three filaments 0.3–0.5 mm long, filaments pubescent, anthers ca. 1 mm long, 2-celled, anther apices acute to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, 0.5–0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed long hairs. Fruits ellipsoid, black, 3–5 × ca. 2 cm, surface smooth; infructescence axis 2–3 mm diam., fruit pedicels not thickened below fruit, not constricted at the apices.

*Flowering time.* April, May, and September.

*Distribution and habitat.* Western Venezuela, western Colombia, southern Ecuador, and Peru (Fig. 9); 2100–3000 m; high montane cloud forest.

*Common names.* Cacao (*Steyermark et al. 100700*), Curo (*C. K. Allen & Terrán 25*) (Venezuela); Roble palta/Sacha palta (*D. N. Smith & Pretel 8004*) (Peru).

*Selected specimens examined.* VENEZUELA. **Mérida:** Carbonera, 22 Jan. 1959 (sterile), *Bernardi 10955* (US). **Tachira:** from La Grita to Pregonero, 2300 m, 9 Oct. 1965 (fl & fr), *Bernardi 10954* (B, C, F, MO, NY). COLOMBIA. **Caldas:** path La Corrala, estate La Zarza, 2440 m, 22 June 1987 (fl), *Velásquez & Marulanda 7754* (MO). **Norte de Santander:** Cordillera Oriental, above Majuey, on road between Chinácota and Toledo, 7°30'N, 72°35'W, 2400–2600 m, 8 Mar. 1986 (fl), *Stein 3635* (MO, NY).



ECUADOR. **Loja:** between Tambo Cachiyacu, La Entrada and Nudo de Sabanillas, 2500–3500 m, 7 Oct. 1943 (immature fr), *Steyermark 54404* (F). **Zamora-Chinchipe:** limit with Podocarpus National Park, 04°23'N, 79°05'W, 2500–2600 m, Jan. 1995 (fl), *Palacios 13147* (MO). PERU. **Amazonas:** Luya Province, Camporredondo-Tullanya, short cut to Cerro Huicsocunga, 2350 m, 3 Sep. 1989 (sterile), *Diaz & Campos 3714* (MO). **Pasco:** Oxapampa Province, Río San Alberto valley, E of Oxapampa, 10°34'S, 75°22'W, 2500 m, 24 July 1984 (immature fr), *D. N. Smith & Pretel 8004* (MO, NY).

Kostermans (1938) placed *Hufelandia latifolia* under *Beilschmiedia sulcata*. However, the type of *H. latifolia* clearly differs from that of *B. sulcata* and is distinguished from the latter by its having erect pubescence, coriaceous leaves, and areoles without free-ending veinlets. *Beilschmiedia sulcata* itself is a problematic species, placed only imperfectly here in this study (see below).

*Beilschmiedia latifolia* is much more similar to *B. ovalis* or *B. towarensis* than to *B. sulcata*. *Beilschmiedia latifolia* and *B. ovalis* share a very similar leaf shape, venation pattern, inflorescence, and flower structure. However, *B. latifolia* has ellipsoid fruits, whereas *B. ovalis* has spherical fruits. In vegetative characters, *B. latifolia* is distinguished from *B. ovalis* by its long hairs on the lower leaf surfaces. Usually, *B. ovalis* has its lower leaf surfaces almost glabrous even when the leaves are young. There are some exceptional specimens in *B. ovalis*, e.g., *Steyermark et al. 98480*, that have densely pubescent leaves with erect hairs when young, but rarely do the leaves retain this pubescence when they are old. Mature leaves of *B. latifolia* sometimes lose the pubescence on the lamina, but leaves of many collections, especially those from Venezuela, remain densely pubescent on the midribs and secondary veins even in old age. See Table 3 for a comparison.

*Beilschmiedia latifolia* and *B. towarensis* are also similar; *B. towarensis* is a complex species with wide vegetative variation (see below), and some collections appear very similar to *B. latifolia*. Nonetheless, *Beilschmiedia latifolia* can be consistently distinguished from *B. towarensis* by its erect hairs. These erect (often wavy) hairs appear on the terminal buds and the lower leaf surfaces, while appressed, sericeous hairs are seen on those parts in *B. towarensis* (see Table 3 for the comparison).

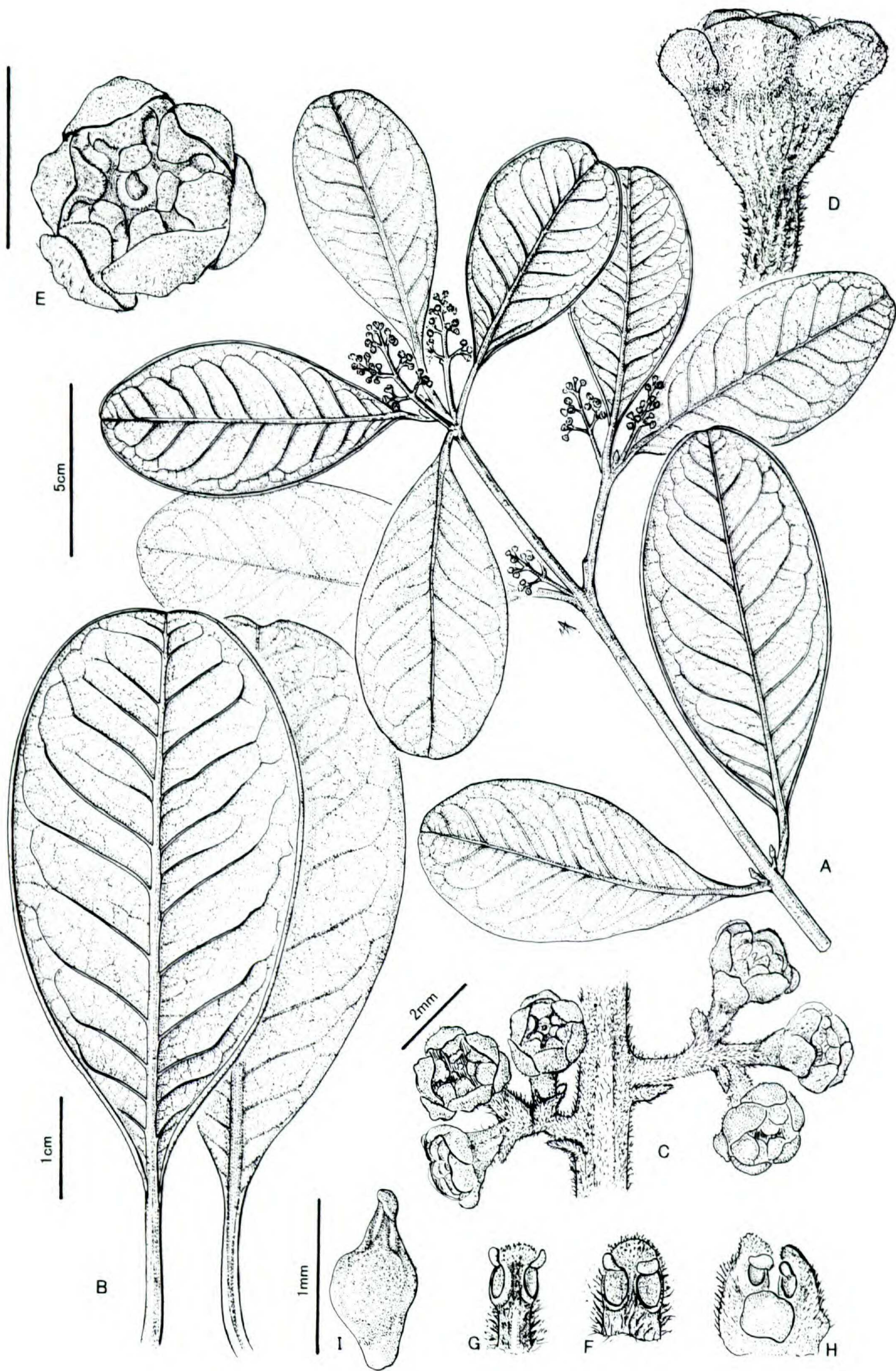
**15. *Beilschmiedia linharensis*** Sa. Nishida & van der Werff, sp. nov. TYPE: Brazil. Bahia: Reserva Florestal da Porto Seguro—CVRD/BA, Aceiro, 2100 km, left side, 26 Oct. 1988 (fl), *Farias 243* (holotype, MO!). Figure 11.

Haec species quoad characteres vegetativos *Beilschmie-*

Table 3. Differences between *Beilschmiedia ovalis* and some species morphologically close to *B. ovalis*. Country abbreviations: Ho = Honduras, CR = Costa Rica, Gu = Guatemala, Me = Mexico, Pa = Panama, Ve = Venezuela, Co = Colombia, Ec = Ecuador, Pe = Peru, Bo = Bolivia.

	<i>B. ovalis</i>	<i>B. latifolia</i>	<i>B. ovalioides</i>	<i>B. steyermarkii</i>	<i>B. tilaranensis</i>	<i>B. towarensis</i>
Geographic distribution	Ho, CR, Pa	Ve, Co, Ec, Pe	Me	Gu	CR, Pa	CR, Pa, Ve, Co, Ec, Pe, Bo
Altitudinal distribution	1800–2800 m	2100–3000 m	1850–2750 m	300–400 m	1100–1580 m	500–2200 m
Pubescence on twigs and leaves	erect, short, and curly	erect, long, and straight to curly	erect, short, and curly	erect, short, and curly	erect, short, and curly	appressed, short, and straight
Leaf shape	ovate to broadly elliptic	ovate to broadly elliptic	obovate to broadly elliptic	narrowly elliptic	obovate	ovate to elliptic to obovate
Typical leaf length (cm)	4–10	7–11	11–16	5–10	6–13	8–20
Typical secondary vein number (pairs)	5 to 9	6 to 9	11 to 14	7 to 8	7 to 11	5 to 11
Pubescence on lower leaf surfaces	glabrous	pubescent	pubescent	glabrous	glabrous	pubescent
Fruit shape	spherical	ellipsoid	spherical	unknown	ellipsoid	ellipsoid







*diae rigidae* similis, sed ab ea foliis angustioribus atque floribus minoribus, ab aliis speciebus neotropiceis floribus depresso globosis differt.

Tree, to ca. 30 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely to densely pubescent with appressed straight hairs. Leaves opposite; petioles 1.5–2 cm long, flat above, slightly darker than twigs, glabrous; blades coriaceous, obovate to elliptic, (5.5–)8–14 × 3–5 cm; base cuneate, inrolled toward lower surface (entire margin slightly inrolled toward lower surface), apex rounded to obtuse; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed or slightly impressed above, raised below, secondary veins 8 to 12 (14) pairs, slightly raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins almost immersed on both sides. Inflorescences in axils of leaves, paniculate with few branches, 2.5–3.5 cm long, relatively densely pubescent with erect straight hairs, with ca. 15 flowers per inflorescence; floral pedicels of the lateral division ca. 0.5 mm long, pedicels of the central flowers up to 1 mm long. Flowers depressed-globose, ca. 1.6(–2) mm long, ca. 2.2 mm diam.; tepals 6, equal, curved toward inside, broadly ovate, ca. 0.5 mm long, ca. 1 mm wide, sparsely pubescent with erect hairs outside, sparsely pubescent with erect hairs to almost glabrous inside, stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.3 mm long, filaments pubescent, anthers ca. 0.5 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands on innermost three stamens globose; staminodia 3, sagittate, ca. 0.3 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits unknown.

*Flowering time.* October.

*Distribution.* Espírito Santo, Brazil (Fig. 12).

*Paratypes.* BRAZIL. **Espírito Santo:** Reserva Florestal de CVRD. Linhares, Est. Cinco-Folhas, 1320 km right side, 16 Nov. 1982 (young fl), *Folli 409* (MO), 6 Oct. 1993 (young fl), *Folli 2033* (MO).

This species was first found in Linhares, Espírito Santo. Although I have only one collection in ma-

ture flower and two collections in flower bud, the small depressed-globose flowers of this species appear unique among neotropical *Beilschmiedia* and are diagnostic for *B. linharensis*. It shares a similar phyllotaxis, blade venation pattern, pubescence type, and leaf shape with *B. rigida*.

**16. *Beilschmiedia manantlanensis*** Cuevas & Cochrane, *Novon* 9: 18. 1999. TYPE: Mexico. Jalisco: municipio de Autlán de Navarro, S of Corralitos, Cañada de Alentrisco, 104°18'20"W, 19°36'19"N, 1800–1900 m, 26 Mar. 1998 (fl), *Guzmán & Santana 1616* (holotype, ZEA not seen; isotypes, BM not seen, CAS not seen, CHAPA not seen, ENCB not seen, F not seen, IBUG not seen, IEB not seen, MEXU not seen, MICH not seen, MO!, NY not seen, TEX not seen, UCR not seen, WIS not seen, XAL not seen).

Tree, to 20–30 m tall. Terminal buds densely pubescent with light brown, erect, long, straight hairs. Twigs terete, densely pubescent with long erect hairs, less densely when older. Leaves clustered (opposite on the tip of the twigs); petioles ca. 1 cm long, flat above, pubescent with long erect hairs to glabrous, concolorous with twigs; blades chartaceous, elliptic to narrowly obovate, 10–14 × 3.5–6 cm; base obtuse, not inrolled, apex obtuse to rounded; upper leaf surface glabrous, lower leaf surface pubescent with long hairs especially along the major veins when young, less densely to glabrous when old, lower surface not glaucous; midrib slightly raised above, raised below, secondary veins about 14 pairs, slightly raised above, raised below, tertiary veins usually not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both surfaces. Inflorescences in axils of leaves, paniculate, 2–3 cm long, pubescent with long erect hairs or glabrous, glaucous, with less than 10 flowers per inflorescence; floral pedicels of the lateral divisions ca. 3 mm long, pedicels of the central flowers 4–7 mm long. Flowers ca. 3 mm long, ca. 3 mm diam., yellowish green; tepals 6, equal, ovate, ca. 1.8 mm long, ca. 1.2 mm wide; slightly pubescent with erect hairs to glabrous on both sides; stamens 9, outer six filaments ca. 0.5

←

Figure 11. *Beilschmiedia linharensis* (Farias 243). —A. Flowering branch. —B. Lower leaf surface (left) and upper leaf surface (right). —C. Part of inflorescence. —D. Lateral view of flower. —E. Flower from above. —F. Stamen of whorl I/II, ventral view. —G. Stamen of whorl III, dorsal view. —H. Stamens of whorl II (right) and whorl III (left) with gland. —I. Pistil.



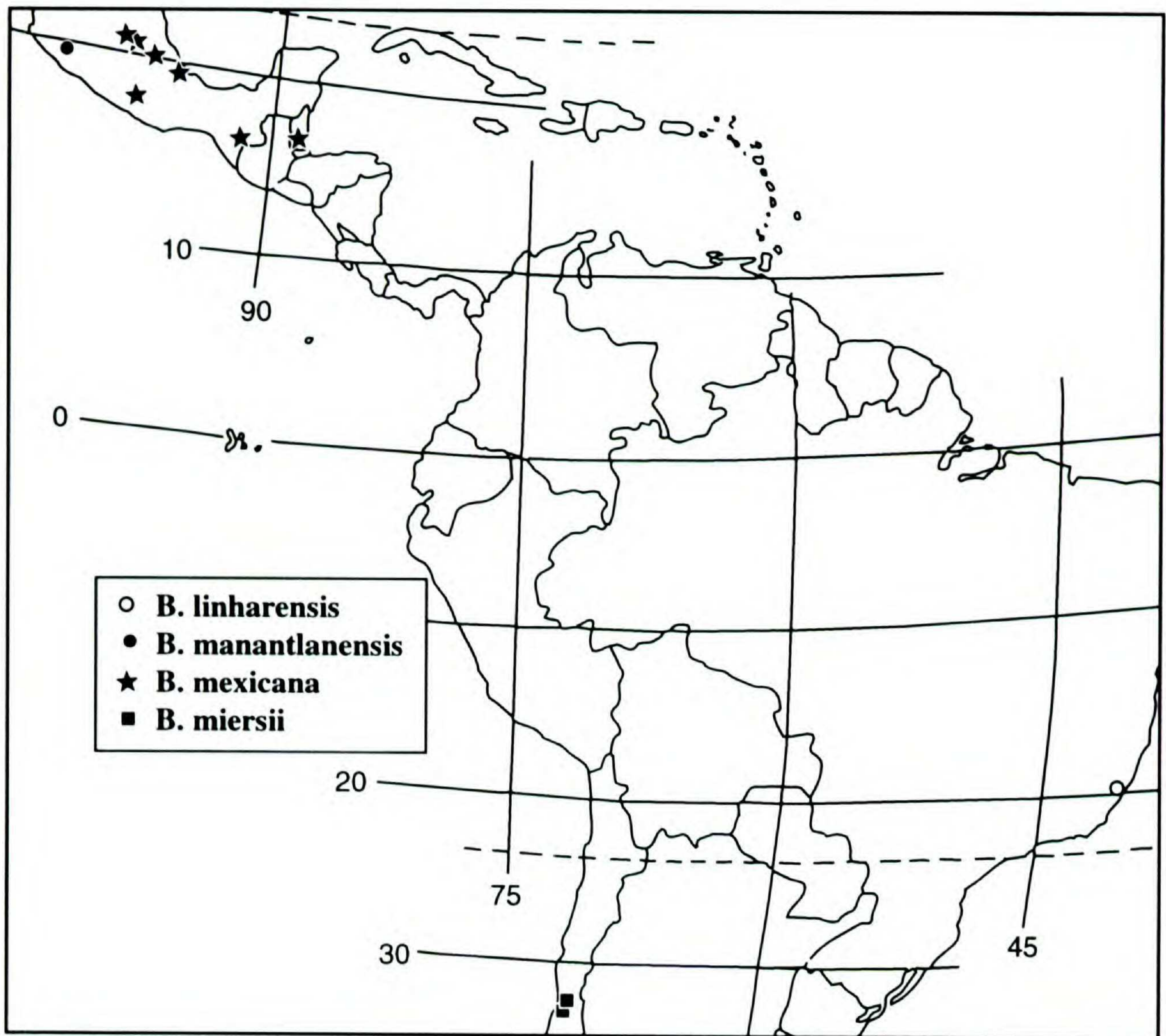


Figure 12. Representative distribution of *Beilschmiedia linharensis*, *B. manantlanensis*, *B. mexicana*, and *B. miersii*.

mm long, innermost three filaments ca. 0.7 mm long, filaments pubescent, anthers ca. 0.8 mm long, 2-celled, anther apices obtuse and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.5 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with erect hairs, glabrous at the bottom. Fruits unknown.

*Flowering time.* March.

*Distribution and habitat.* Jalisco, Mexico (Fig. 12), at 1800–1900 m in montane mesophyll forest.

*Specimen examined.* MEXICO. **Jalisco:** municipio de Autlán de Navarro, S of Corralitos, Cañada de Alentrisco, 104°18'20"W 19°36'19"N, 1900 m, 9 Mar. 1991 (fl), *Cuevas et al.* 4076 (MO).

This species probably belongs to the *Beilschmiedia hondurensis* group. It has erect pubescence on the terminal buds and long leaves with coarse blade venation, approaching *B. angustielliptica*. It differs from *B. angustielliptica* in its leaf arrangement (clustered), leaf shape (with roundish to obtuse

apex), and floral pedicels (being about twice as long as those of *B. angustielliptica*). *Beilschmiedia manantlanensis* also tends to have staminal filaments more pubescent than *B. angustielliptica* or others within the *B. hondurensis* group.

**17. *Beilschmiedia mexicana* (Mez) Kosterm.,** Rec. Trav. Bot. Néerl. 35: 846. 1938. *Hufelandia mexicana* Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 20. 1889. TYPE: Mexico. Orizaba, 1853 (fr), *F. Müller 1460* (lectotype, designated by Kostermans (1938), K!; isoelectotypes, B not seen, K!, LE not seen, W not seen).

*Linociera areolata* Lundell, Amer. Midl. Naturalist 23: 176. 1940. TYPE: Mexico. Hidalgo: above Chapulhuacan, 1300 m, 12 July 1937 (fr), *Lundell & Lundell 7165* (holotype, AFS not seen; isotype, F!).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs, rarely almost glabrous. Twigs terete, compressed when young, pubescent with appressed hairs or glabrescent, less densely pubes-



cent to glabrous when older. Leaves alternate, petioles 0.5–2 cm long, flat to canaliculate above, glabrous, rarely pubescent with appressed hairs, concolorous with twigs; blades chartaceous, elliptic, sometimes asymmetric, 5–13(–19) × 3–8(–10) cm; base cuneate, not inrolled, apex acute to obtuse, rarely acuminate; leaf surface glabrous on both sides; lower leaf surface not glaucous, or very rarely glaucous; midrib and secondary veins almost immersed or slightly raised above, raised below, secondary veins in 6 to 11 pairs, tertiary veins not percurrent, minor venation pattern fine, areoles rounded and lacking free-ending veinlets inside, tertiaries and minor veins raised on both sides, very rarely immersed above. Inflorescences in axils of leaves, paniculate, 1–10(–16) cm long, sparsely pubescent with short straight hairs or almost glabrous, with 10 to 20 (45) flowers per inflorescence; floral pedicels of the lateral divisions (0.3–)1–1.5 mm long, pedicels of the central flowers up to 4(–5.5) mm long. Flowers 2.5–2.7 mm long, 2.5–3 mm diam.; tepals 6, equal, ovate to elliptic, 1.3–1.7 mm long, 1.2–1.5 mm wide, sparsely pubescent with erect to appressed hairs on both surfaces. Stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers ca. 0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.5 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purplish black, 2.5–3(–4) × ca. 1.5 cm, surface smooth; infructescence axis 1–2.5 mm diam., fruit pedicels scarcely thickened below the fruits, slightly constricted at the apices.

*Flowering time.* March to June, September.

*Distribution and habitat.* Southern Mexico and Belize (Fig. 12); 800–1780 m; montane mesophyll forest or semideciduous forest, rarely on limestone.

*Common names.* Calanique (A. Gómez P. 795), Tzitztez (A. Méndez G. & Shilom 7686) (Mexico).

*Selected specimens examined.* MEXICO. **Chiapas:** Municipio Oxchuc, waterfall of Río Mesbiljaz, 15 June 1984 (fr), A. Méndez G. & Shilom 7686 (MO). **Guerrero:** Municipio Atoyac de Alvarez, in Nueva Dhlhi, 17 km NE of El Paraíso, 1390 m, 29 Mar. 1983 (fl & immature fr), Soto & Martínez 5122 (MO). **Hidalgo:** Municipio Tlanchinol, road to Tierra Colorada, 1580 m, 9 Apr. 1992 (immature fr), Luna & Ocegueda 323 (MEXU). **Puebla:** Municipio Ahuacatlán, Agua Dulce, 4 km SE of Ahuacatlán, 20°01'N, 97°50'W, 1180 m, 12 June 1985 (immature fr), Tenorio et al. 9000 (MO). **Queretaro:** Municipio Landa, 0.5 km SE of El Aguacate, 1520 m alt., 19 Dec. 1988 (fl), Rubio 362 (IEB, MEXU). **San Luis Potosí:** Municipio

Xilitla, 2 km SE of Ahuacatlán, 1300 m, 27 June 1959 (fl), Rzedowski 10975 (MEXU). **Veracruz:** Cosalapa, Mar. 1922 (fl), Purpus 8745 (MO, NY, US). BELIZE. **Toledo:** Maya Mountains, Bladen Nature Reserve, upper Bladen Branch basin, 16°30'41"N, 88°56'52"W, 900 m, 12 May 1996 (immature fr), Holst et al. 5236 (MO).

*Beilschmiedia mexicana* appears close to *B. pendula*, sharing similar floral characters. However, *B. mexicana* usually has minor leaf venation conspicuously raised on both sides, acute leaf apices, and non-glaucous lower leaf surfaces, whereas *B. pendula* displays minor venation immersed above (although the pattern is visible), acuminate leaf apices, and glaucous lower leaf surfaces. These two species also have different minor venation patterns: *B. mexicana* has areoles rounded and lacking free-ending veinlets inside, while *B. pendula* has areoles angular and subtending branched veinlets. A distribution gap exists between them, with *B. pendula* found from Nicaragua to Ecuador and the West Indies and *B. mexicana* from Mexico and Belize.

**18. *Beilschmiedia miersii* (Gay) Kosterm., Rec. Trav. Bot. Néerl. 35: 860. 1938. *Bellota miersii* Gay, Fl. Chil. 5: 298. 1851 or 1852. TYPE: Chile. Valparaiso: Aconcagua, (fl), Gay 236 (lectotype, designated by Kostermans (1938), P!).**

Tree, to 25 m tall. Terminal buds densely pubescent with erect curly hairs, or rarely with erect, slightly wavy hairs. Twigs terete, compressed when young, pubescent with erect, curly to wavy hairs, usually densely so when young, less densely pubescent when old. Leaves opposite; petioles 0.3–1 cm long, sulcate to canaliculate or rarely flat to terete above, pubescent with erect, curly to wavy hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish ovate, (2.5–)5–12 × 1.5–6.5 cm; base rounded to obtuse, flat or rarely slightly inrolled toward lower surface, apex obtuse to rounded, sometimes retuse; leaf surface glabrous on both sides, rarely sparsely pubescent along the midrib; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins (5) 7 to 8 (10) pairs, slightly raised or almost immersed above, slightly to conspicuously raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised or almost immersed above, slightly raised below. Inflorescences in axils of leaves (sometimes two inflorescences from one axil of the leaf), paniculate with few branches, 2–6(–9) cm long, ± densely pubescent with erect curly hairs, with 10 to 35 flowers per inflorescence; floral pedicels of the lateral di-



visions 0.5–1 mm long, pedicels of the central flowers up to 3.5 mm long. Flowers 2.5–3 mm long, 3.2–3.5(–4.2) mm diam.; tepals 6, equal, ovate, 1.2–1.5(–2.2) mm long, 1.2–1.7(–2.5) mm wide,  $\pm$  densely pubescent with erect curly hairs outside, densely pubescent with long erect hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three stamens ca. 0.3 mm long, filaments pubescent, outer six anthers 0.7–1 mm long, inner three anthers 0.6–0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.5 mm long; pistil 1.4–1.6 mm long, glabrous or rarely sparsely pubescent, ovary longer than and gradually narrowed into the style; receptacle pubescent with long appressed hairs. Fruits ellipsoid, up to 4  $\times$  3 cm (fide Kostermans, 1938), surface smooth; fruit pedicels in mature fruit unknown.

*Flowering time.* January to June and October to November.

*Distribution.* Central Chile (Fig. 12) at 120–900 m; reported to grow in subtropical, semiarid vegetation (Heusser, 1971).

*Common name.* Bellota (*Miers s.n.*).

*Selected specimens examined.* CHILE. **Valparaiso:** Zapallar, stream of Tigre, 27 Feb. 1952 (fl), *Boelcke 6466* (F, MO). **Santiago:** Acules, Apr. 1902 (fl), *Remy 108* (BM, MO).

*Beilschmiedia miersii* is one of only two *Beilschmiedia* species from Chile; both Chilean species are discussed under *B. berteriana*.

Nees (1836) used the name *Boldu chilinum* supposedly when citing a collection of this species, but it is to be treated as a superfluous name of *Boldus chilensis*, whose type belongs in the Monimiaceae.

Two collections of this species in flower, *Zöllner 11607* and *Anonymous (Nr.?) 547*, have a foliose bract on the rachis, also rare for neotropical *Beilschmiedia* species. However, this character is not consistently seen in this species.

**19. *Beilschmiedia ovalioides*** Sa. Nishida, sp. nov. TYPE: Mexico. Oaxaca: Ixtlán District, Sierra de Juárez, en route from Xiacui to Talea de Castro, ca. 25 km SSW of Talea from the route, 2750 m, 19 Apr. 1982 (fl & fr), *Lorence & Cedillo 4078* (holotype, MEXU!; isotypes, F!, MO!). Figure 13.

Haec species *Beilschmiediae ovali* affinis, sed ab ea foliis majoribus infra puberulis, nervis pluribus, venis tertiariis percurrentibus atque petiolis longioribus differt.

Tree, to 35 m tall. Terminal buds densely pubescent with ferruginous, short erect curly hairs. Twigs terete, slightly angular when young, densely pubescent with ferruginous, short erect curly hairs. Leaves alternate; petioles 2–3 cm long, flat above, rarely slightly canaliculate above, pubescent with ferruginous short curly hairs, less densely pubescent when old, concolorous with twigs; blades coriaceous, broadly elliptic to obovate, sometimes slightly asymmetric, (8–)11–16  $\times$  5–10 cm; base obtuse to cuneate, not inrolled, apex acute to acuminate; upper leaf surface glabrous, lower leaf surface puberulent with short erect hairs; lower surface usually glaucous; midrib and secondary veins immersed above, raised below, secondary veins 11 to 14 pairs, tertiary veins percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above, slightly raised or immersed below (venation pattern visible below). Inflorescences in axils of leaves near terminal buds, paniculate, 4.5–12 cm long, pubescent with ferruginous, short erect curly hairs, with 40 to 80 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 1 mm long. Flowers greenish yellow, ca. 2.8 mm long, ca. 3 mm diam.; tepals 6, equal, ovate, 1.8–2.2 mm long, 1.2–2 mm wide, densely pubescent with erect hairs outside, sparsely pubescent with erect curly hairs to almost glabrous inside; stamens 9, filaments 0.3–0.8 mm long, pubescent, anthers ca. 0.9 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm; pistil ca. 2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with long, appressed to erect hairs. Fruits spherical, black, 3–4  $\times$  3–4 cm, surface smooth; infructescence axis ca. 5 mm diam., fruit pedicels thickened to 10 mm in diam. below the fruit, not constricted at the apices.

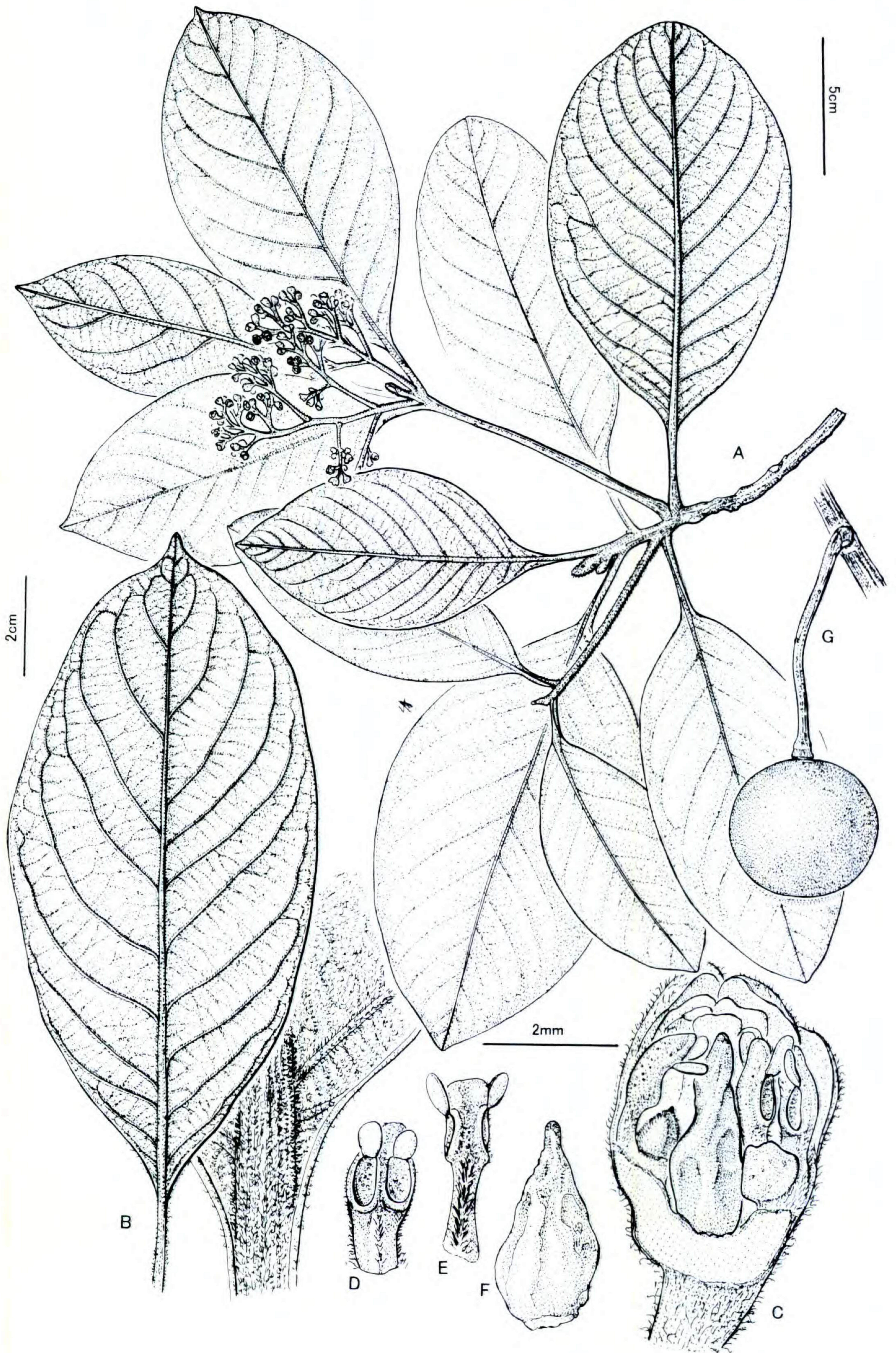
*Flowering time.* April, May, and August.

*Distribution and habitat.* Southern Mexico (Fig. 14); 1850–2750 m; montane mesophyll forest.

*Paratypes.* MEXICO. **Chiapas:** Municipio Unión Juárez, in El Volcán Tacaná by a road from Talquián to the top of the volcano, along the border with Guatemala,

Figure 13. *Beilschmiedia ovalioides* (Lorence & Cedillo 4078). —A. Flowering branch. —B. Lower leaf surface with detail of pubescence. —C. Flower with tepals removed, showing stamens, gland (right), staminode (left), and pistil. —D. Stamen of whorl I/II, ventral view. —E. Stamen of whorl III, dorsal view. —F. Pistil. —G. Fruit.







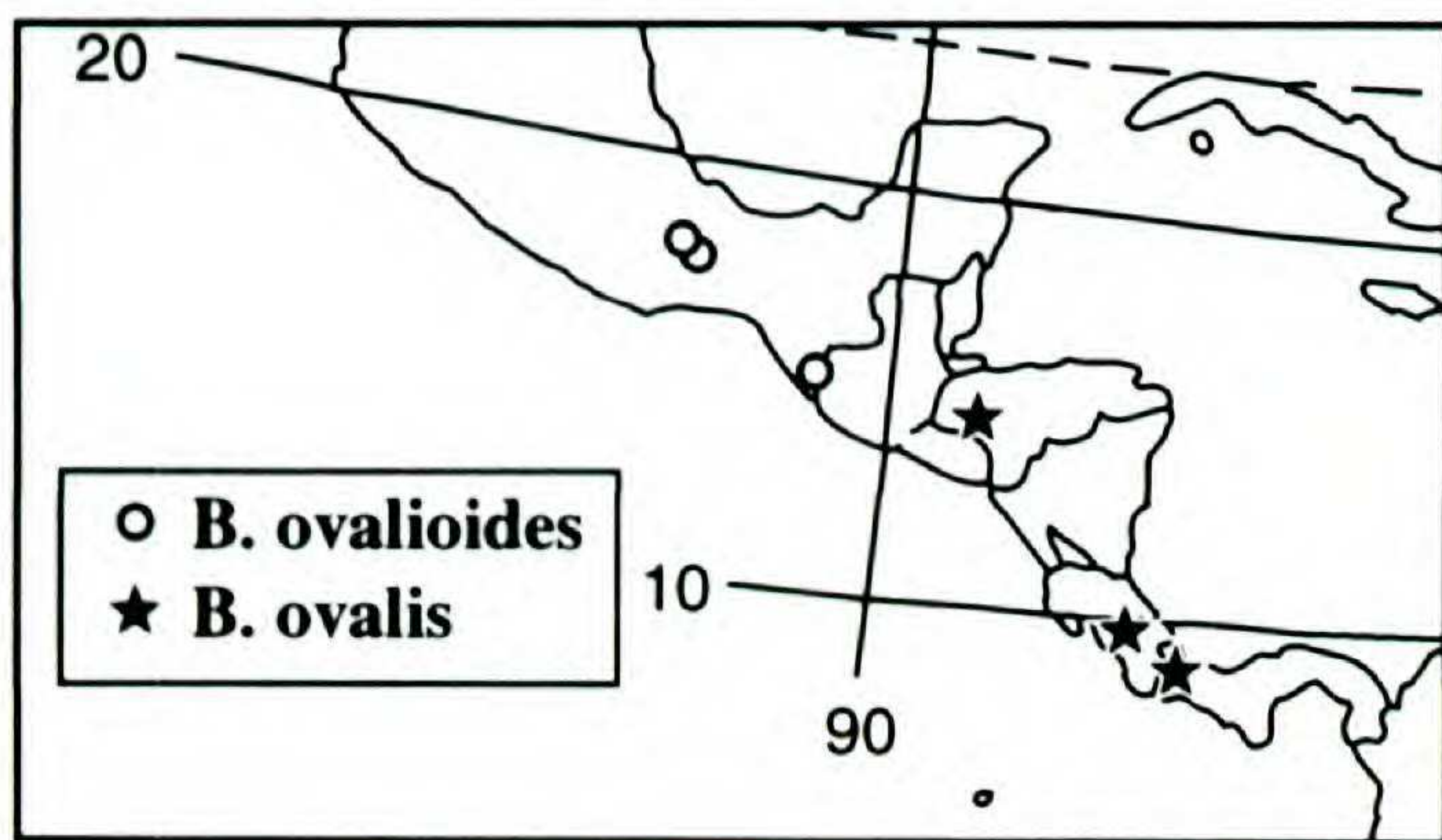


Figure 14. Representative distribution of *Beilschmiedia ovalioides* and *B. ovalis*.

2200–2700 m, 4 Feb. 1987 (fr), *Martínez et al.* 19456 (MO). **Oaxaca:** Sierra de Juárez, ca. 25 km SSW of Talea de Castro, or 3 km N of the junction to Yalina, 2750 m, 31 May 1983 (fl), *Cedillo & Lorence* 2372 (F, MEXU, MO); W of Municipio San Felipe Usila, 8 km straight S from Santa Cruz Tepetotutla, 17°40'06"N, 96°33'24"W, 2395 m, 31 Mar. 1994 (young fl), *Gallardo et al.* 1007 (MEXU); Choapam District, road from Totontepec to Comaltepec, 5 km NE of Totontepec, 1850 m, 11 Nov. 1983 (fr), *Lorence et al.* 4376 (F, MEXU, MO); 20 km SE of Totontepec, 250 m (mistake for 2500 m?), 9 Aug. 1977 (fl), *Sousa et al.* 7871 (UC); Villa Alta District, 8.1 km N of Maravillas, road between Talea de Castro and Yalina, 2370 m, 15 May 1983 (fl & fr), *Torres et al.* 2947 (F, MEXU, MO); Municipio San Felipe Usila, 7.3 km S (179°) of Santa Cruz Tepetotutla, 17°40'23"N, 96°33'28"W, 2220 m, 15 May 1994 (fr), *Rincón* 419 (MEXU); same municipio, 7.6 km S (179°) of Santa Cruz Tepetotutla, 17°40'13"N, 96°33'28"W, 2240 m, 16 May 1994 (fl), *Rincón* 433 (MEXU).

*Beilschmiedia ovalioides* appears close to *B. ovalis*. Both share very similar pubescence type, venation pattern, flower structure, and fruit shape. *Beilschmiedia ovalioides* has longer petioles (more than 2 cm long), lower leaf surfaces puberulent even when old, secondary veins more than 11 pairs, and conspicuously percurrent tertiary veins. *Beilschmiedia ovalis* has shorter petioles (less than 1.5 cm long), lower leaf surfaces glabrous when old, secondary veins less than 9 pairs, and tertiary veins not conspicuously percurrent. Those characters are not diagnostic individually, but in combination they discriminate these two species clearly. *Beilschmiedia ovalioides* tends to have larger (more than 11 cm long), broadly elliptic to obovate leaves, whereas *B. ovalis* usually has smaller (less than 10 cm), ovate leaves. Both species occur above 1800 m, but with some disjunction of distribution. *Beilschmiedia ovalioides* has been collected only in Mexico, whereas *B. ovalis* has been collected in Honduras, Costa Rica, and Panama.

**20. *Beilschmiedia ovalis*** (S. F. Blake) C. K. Allen, *J. Arnold Arbor.* 26: 418. 1945. *Hufelandia ovalis* S. F. Blake, *J. Wash. Acad. Sci.* 9: 461. 1919. TYPE: Costa Rica. Alajuela: Volcán de Poás, 2300 m, 31 Mar. 1907 (fl), *Pittier* 2040 (holotype, US!; isotype, F!).

*Beilschmiedia austin-smithii* (Standl.) C. K. Allen, *J. Arnold Arbor.* 25: 418. 1945. *Persea austin-smithii* Standl., *Field. Mus. Publ. Bot.* 18: 1552. 1938. TYPE: Costa Rica. Alajuela: Cantón de Alfaro Ruiz, Palmira, 30 Apr. 1937 (fl), *A. Smith* 4168 (holotype, F!).

Tree, to 30 m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete to angular, densely to sparsely pubescent with short curly hairs, less dense to glabrous when old. Leaves alternate; petioles 1–1.5 cm long, flat above, glabrous or rarely pubescent with short curly hairs, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, 4–10(–14) × 3–8(–10.5) cm; base obtuse to rounded, not inrolled, apex obtuse; leaf surface glabrous on both sides, rarely partly pubescent with erect curly hairs when young; lower surface glaucous; midrib immersed above, raised below, secondary veins 5 to 9 pairs, immersed above, raised below, tertiary veins not percurrent or weakly percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed or slightly raised above, slightly to conspicuously raised below. Inflorescences in axils of leaves or sometimes clustered around the terminal buds, paniculate, 3–15 cm long, pubescent with erect hairs, with 20 to 50 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 2 mm long. Flowers yellowish, 2.5–3.2 mm long, 2.9–3.7 mm diam.; tepals 6, equal, ovate to elliptic, 1.4–2.3 mm long, 1–1.7 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments 0.5–0.7 mm long, filaments pubescent, anthers ca. 1 mm long, 2-celled, anther apices obtuse and glabrous, glands of the innermost three stamens globose; staminodia sagittate, 0.5–1 mm long; pistil 1.3–1.7 mm long, glabrous, ovary almost as long as or longer than and gradually narrowed into the style; receptacle relatively densely pubescent with long, erect to almost appressed hairs. Fruits spherical, green when immature, ca. 3.5 × ca. 3.5 cm (or bigger), surface smooth; fruit pedicels ca. 5 mm diam., thickened to ca. 10 mm diam. below the fruit, not apically constricted.

*Flowering time.* February to May, September, and November.



*Distribution and habitat.* Western Honduras, central Costa Rica, western Panama (Fig. 14); 1800–2800 m; cloud forest.

*Common names.* Aguacate negro (*E. A. Lao 395*) (Costa Rica), Aguacatillo (*Thomas 584*) (Honduras).

*Selected specimens examined.* HONDURAS. **Comayagua:** 10.5 km E of lago Yojoa, Cerro Azul Meámbar, on the ridge leading to the Cerro Azul peak, 14°48'N, 87°53'W, 1870 m, 12 Mar. 1993 (immature fr), *Thomas 584* (MO). COSTA RICA. **Alajuela:** Palmire, 1900 m, 27 May 1938 (fl), *A. Smith NY675* (F, NY). **Heredia:** Volcán Barba, 1800–2000 m, 14 Nov. 1971 (sterile), *Holdridge 6595* (CR, NY). **San José:** Cantón Aserrí, valley of Río Grande de Tárcoles, El Cedral, Alto Hierbabuena, 9°50'30"N, 84°06'35"W, 2150 m, 6 Nov. 1993 (sterile), *J. F. Morales 1952* (INB, MO). PANAMA. **Chiriquí:** Cerro Punta, 2000 m, 24 May 1946 (fl?, missing), *P. H. Allen 3490* (MO).

Kostermans (1938) regarded *Hufelandia ovalis* as a synonym of *Beilschmiedia sulcata*, but Allen (1945) reestablished it as *B. ovalis*. However, Allen did this without seeing the type of *H. ovalis*, and in the same paper she described a new species, *B. austin-smithii*, based on a collection actually conspecific with *B. ovalis*. The type collection of *B. austin-smithii* has denser pubescence on the petioles and lower leaf surfaces than typical for *B. ovalis*, probably because this type has relatively young leaves: no other significant differences are observed.

*Beilschmiedia ovalis* belongs to the *B. costaricensis* group and is distinguished by its short curly pubescence on the terminal buds and twigs, alternate, coriaceous, ovate to broadly elliptic and glabrate (when old) leaves, and spherical fruits. This species shares similar leaf shape with *B. latifolia* and *B. towarensis*, similar pubescence type with *B. steyermarkii* and *B. tilaranensis*, and similar reproductive characters with *B. ovalioides*. For differences between *B. ovalis* and each of these five species, see Table 3 and the discussion under the five species, respectively.

**21. *Beilschmiedia pendula*** (Sw.) Hemsl., Biol. Cent.-Amer., Bot. 3: 70. 1882. *Laurus pendula* Sw., Prodr.: 65. 1788. *Hufelandia pendula* (Sw.) Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 22. 1833. TYPE: Jamaica: locality unknown, (fl), *Swartz s.n.* (lectotype, designated by Kostermans (1938), S not seen; islectotypes, BM!, C!).

*Hufelandia thomaea* Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 23. 1833. TYPE: St. Thomas. Locality and collector unknown (B not seen, P not seen).

Tree, to 35 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, pubescent with appressed straight hairs, less densely pubescent to glabrous when old. Leaves alternate; petioles 0.7–2 cm long, flat or rarely canaliculate above, glabrous or sparsely pubescent with appressed hairs, concolorous with the twigs; blades firmly chartaceous, elliptic to oblanceolate, 4–13(–22) × 2–5(–10.5) cm; base cuneate, not inrolled, apex acuminate or very rarely acute to obtuse; upper leaf surface glabrous, lower leaf surface glabrous or rarely sparsely pubescent with appressed hairs; lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins (5–)7–10(–12) pairs, immersed above, slightly to conspicuously raised or rarely almost immersed below, tertiary veins not percurrent or rarely ± percurrent, minor venation pattern fine, areoles angular with branched free-ending veinlets inside, tertiaries and minor veins immersed above (but the pattern partially visible), almost immersed or slightly raised below, the pattern visible on the upper surface much coarser than on the lower surface. Inflorescences in axils of leaves, paniculate with few branches, 3–14(–17) cm long, almost glabrous or sparsely pubescent with short appressed hairs, with 5–25(–40) flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.5 mm long, pedicels of the central flowers up to 4 mm long. Flowers greenish yellow to whitish, 2–3 mm long, 2.3–2.8 mm diam.; tepals 6, equal, ovate, 1.2–1.7 mm long, 0.8–1.4 mm wide, sparsely pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3–0.4 mm long, innermost three filaments 0.4–0.6 mm long, filaments pubescent, anthers ca. 0.8 mm, 2-celled, anther apices obtuse-acute to truncate and glabrous, glands of the innermost stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.5 mm long, glabrous or rarely sparsely pubescent, ovary almost as long as and gradually narrower into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, shiny, ca. 2–3.5(–4.5) × ca. 1.5 cm, surface smooth; infructescence axis ca. 2 mm diam., fruit pedicels strongly constricted at the apices, slightly thickened below the fruit.

*Flowering time.* February to November.

*Distribution and habitat.* Honduras, Nicaragua, southern Costa Rica, Panama, the West Indies, Venezuela, Colombia, and Ecuador (Fig. 15); 0–1680 m; montane broad-leafed forest, tropical wet forest, sometimes on limestone.

*Common names.* Mulato (*Ekman 14826*), Carne de doucella (*A. Luna 650*) (Cuba); Vacarita (*Stern*



& Chambers 173) (Panama); Cobalongo macho (Veillon II/12) (Venezuela).

*Selected specimens examined.* CUBA. **Camagüey:** Loma del Gato and vicinity Cobre Range of Sierra Maestra, 11 July–14 Aug. 1921 (immature fr), *León et al.* 10451 (NY). **Cienfuegos:** SE of Cumanayagua, Sierra de San Juan, 3–400 m, July 1941, (fl), *Howard* 5695 (F, MO, NY, U). **Guantánamo:** E Cuba, Monte Verde, 1856–7 (fl & immature fr), *Wright* 485 (BM, BR, MO, NY). **Holguín:** Pierra de Nipe, at Río Piedras, 500 m, 24 Aug. 1915 (immature fr), *Ekman* 6402 (F, NY, US). **Sancti Spíritus:** Santa Clara, Mts. Trinidad, 650–750 m, 9 Mar. 1910 (fl), *Britton & Wilson* 5320 (NY). **Santiago de Cuba:** S side of the crest of the Sierra Maestra, La Bayamesa, W of Aserradero San Antonio de los Cumbres, 1400–1500 m, 23–24 Jan. 1956 (young fl), *Morton* 9563 (US). **Villa Clara:** St. Domingo, 600 m, 24 May 1887 (fl), *Eggers* 2087 (NY). JAMAICA. Clarendon, along road between Ritchies & Balcarres, 900 m, 10 Nov. 1973 (immature fr), *Proctor* 33607 (MO). HAITI. Ouest, Gros Cheval, Mornes des Commissaires, 1400 m, 17 Mar. 1942 (immature fr), *Holdridge* 1053 (BM, F, MO, NY, US). DOMINICA. Barahona, El Gajo, ca. 7 km from the carretera de Cabral a Polo, through the way to Entrada de Cortico (Monteada Nueva), 18°07.5'N, 71°13.5'W, 1400 m, 18 Jan. 1986 (immature fr), *Zanoni & Pimentel* 36009 (MO, NY). PUERTO RICO. Adjuntas, in a forest near a stream of Yunro, 22 May 1886 (fl), *Sintenis* 4398 (B, BM, BR, NY, P, US). ST. KITT. Lawrent? estate, 8 Sep.–5 Oct. 1901 (immature fr), *Britton & Cowell* 634 (NY). MONTSERRAT. Centre Hills, 400 m, 7 Nov. 1944 (fl), *J. S. Beard* 409 (NY, U). GUADELOUPE (and dependances). St. Louis, valley of St. Louis, 700 m, 18 Sep. 1899 (fl), *Duss* 4014 (4006) (NY). MARTINIQUE. Pinte-Notie, 300–700 m, 1897 (young fl & fr), *Duss* 3863 (NY). ST. LUCIA. Fouds St. La eques, 26 Mar. 1889 (sterile), *Anonymous s.n.* (BM). HONDURAS. **Yoro:** road Real de San José Texíquat to Campo Nuevo at a place called Las Letras, W of Cerro Cabeza de Negro, 15°28'00"N, 87°26'05"W, 1010 m, 24 Apr. 1995 (fr), *Aguilar & Evans* 4073 (MO). NICARAGUA. **Matagalpa:** Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, slopes N of Hda. San Martín, ca. 13°14'–15'N, 85°39'W, 950–1100 m, 24 Nov. 1981 (fr), *Stevens et al.* 20891 (MO). COSTA RICA. **Puntarenas:** Buenos Aires, Cordillera de Talamanca, Ujarrás, left margin of Quebrada Dorora, enroute to Río Lori, 09°17'50"N, 83°15'30"W, 1520 m, 11 Mar. 1993 (fl), *Herrera* 5861 (MO). **San José:** along Pan American Highway, ca. 1 km N of San Isidro del General, ca. 600 m, 9 Sep. 1943 (sterile), *Barbour* 1019 (F). PANAMA. **Darién:** Bahía de Piñas, slopes of bordering hills, 24 June 1957 (sterile), *Stern & Chambers* 173 (NY). **Panamá:** Sendero de Interpretación, 1 km E of camp in the reserve forest of Inrenare, 8°40'N, 79°55'W, 800–900 m, 24 Mar. 1994 (fl), *Correa & Montenegro* 10408 (MO). VENEZUELA. **Mérida:** Highway Panamericana, between Río Gavilan & Río Perdido, 150–500 m, 2 June 1960 (fr), *Veillon II/12* (MO). **Miranda:** Distrito Paéz, road between San Juan–Montevideo, 10°04'–06'N, 65°45'–47'W, 400 m, 7 Sep. 1977 (young fl), *A. González & Ortega* 1363 (MO). COLOMBIA. **Antioquia:** Municipio San Luis, stream La Cristalina, 6°N, 74°45'W, 730–770 m, 22 May 1987 (immature fr), *Guillermo & Cárdenas* 933 (MO). **Nariño:** Espriella, Fumaeo, 22 June 1951 (fr), *Castañeda* 2820 (F). ECUADOR. **Esmeraldas:** San Lorenzo, near rail road, right of way 3 km SE, 20 Apr. 1943 (young fl & immature fr), *Little, Jr.*

6294 (MO, NY, US). **Napo:** 5 km N of Coca, El Chunchu Floristic Reserve, 0°25'S, 77°01'W, 250 m, 23 May 1993 (young fl), *Palacios* 10794 (MO).

Kostermans (1938) recognized Bentham as the author of the combination *Beilschmiedia pendula*, but Bentham did not validly publish it since he did not definitely associate the epithet *pendula* with the generic name *Beilschmiedia*. Hemsley was the author who validly published the combination in 1882.

Nees (1833) established *Hufelandia thomaea* on account of its upright inflorescence and non-pendulous fruits. However, Meisner (1864) did not recognize the differences and submerged it in *Beilschmiedia pendula*. The type of *H. thomaea* was not available for this study, but Meisner's treatment should be supported because the characters Nees referred to are too subtle to discriminate these taxa.

*Beilschmiedia pendula* is one of the most widely distributed neotropical species in the genus. It is often confused with *B. costaricensis*, *B. mexicana*, and *B. towarensis*: these four species share similar pubescence type, leaf shape (except for a group of *B. towarensis* with ovate to broadly elliptic leaves), flower structure, and fruit shape. However, *B. pendula* can be distinguished from *B. costaricensis* by blade venation almost immersed on upper leaf surfaces, glaucous lower leaf surfaces, and its fruit pedicels apically constricted. Differences between *B. pendula* and *B. mexicana* or *B. towarensis* are discussed under these two species respectively.

Leaves of *B. pendula* are usually small and narrowly elliptic-oblongate. However, some exceptional collections show large and wide leaves, especially from Puerto Rico and Martinique. Leaf apices in these collections also differ from typical, distinctively acuminate leaf apices in being obtuse.

**22. *Beilschmiedia rigida* (Mez) Kosterm.,** *Rec. Trav. Bot. Néerl.* 35: 856. 1938. *Hufelandia rigida* Mez, in Taubert, *Bot. Jahrb. Syst.* 17: 519. 1893. TYPE: Brazil. Rio de Janeiro: Alto Macaé de Nova Friburgo, Oct.–Nov. (fl), *Glaziou* 19790 (lectotype, designated by Kostermans (1938), B not seen; isolectotypes, BM!, C!, F!, LE not seen, P!).

Tree, height unknown. Terminal buds pubescent with appressed short straight hairs. Twigs terete, sparsely pubescent with appressed short straight hairs or almost glabrous. Leaves opposite; petioles 1.5–3.5 cm long, flat above, slightly discolored from twigs, glabrous; blades coriaceous, obovate, 14–22 × 7–11 cm; base decurrent, flat to slightly inrolled toward lower surface, apex rounded to obtuse; leaf



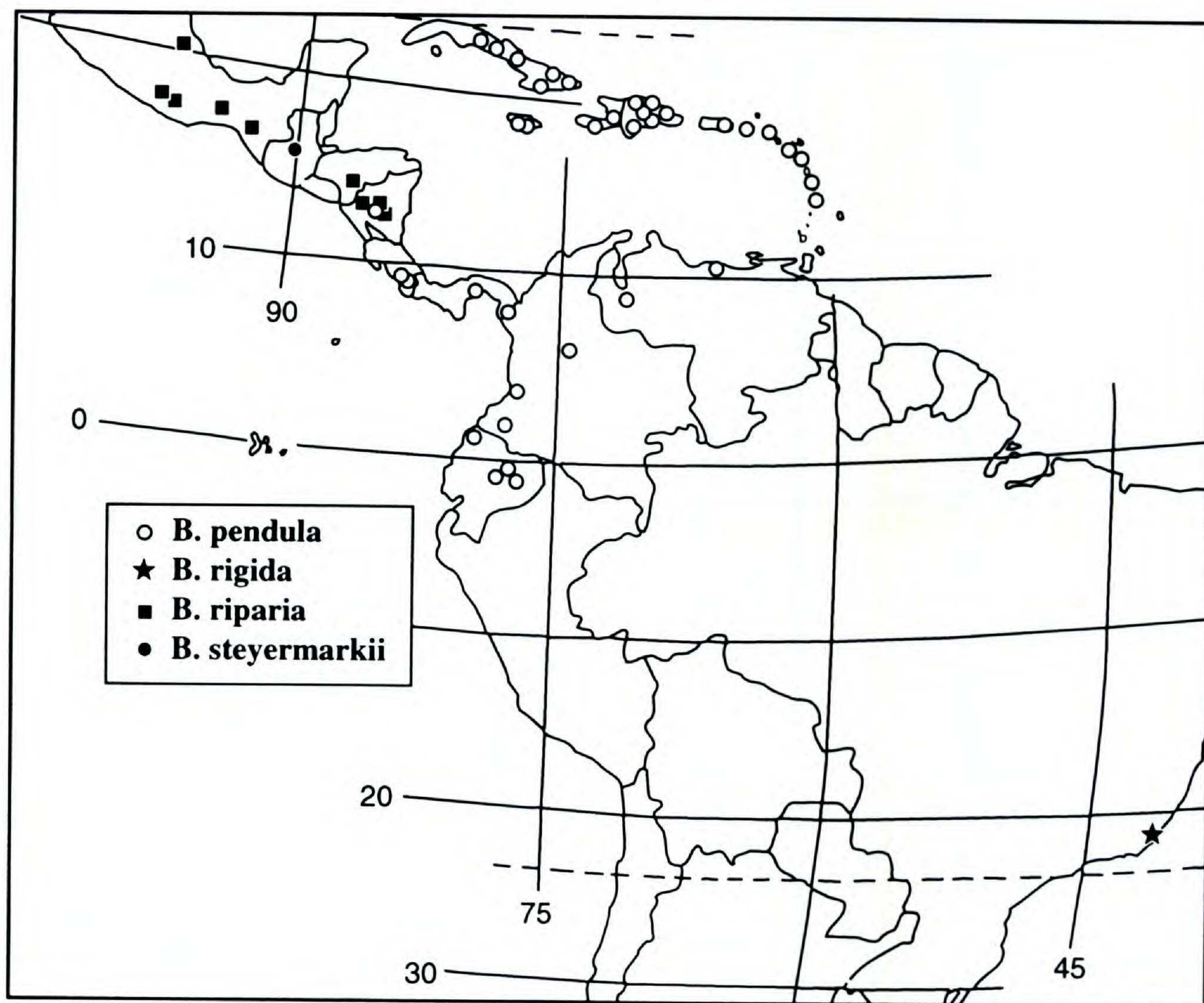


Figure 15. Representative distribution of *Beilschmiedia pendula*, *B. rigida*, *B. riparia*, and *B. steyermarkii*.

surface glabrous on both sides; lower leaf surface not known whether glaucous or not; midrib immersed above, raised below, secondary veins 9 to 12 pairs, slightly raised above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both sides. Inflorescences in axils of leaves or clustered around the terminal buds, paniculate, 4–12 (–18) cm long, sparsely pubescent with appressed to erect hairs or almost glabrous, with 10 to 30 (55) flowers per inflorescence; floral pedicels of the lateral divisions 1.5–2 mm long, pedicels of the central flowers up to 5 mm long. Flowers 3–3.5 mm long, ca. 3.5 mm diam.; tepals 6, equal, ovate, 1.5–2.3 mm long, 1.1–1.5 mm wide, pubescent with erect hairs on both surfaces; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.9–1.2 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands on innermost three stamens globose; staminodia 3, sagittate, ca. 0.7 mm long; pistil 1.6–1.9 mm long, pubescent, ovary slightly longer than and gradually

narrowed into the style; receptacle pubescent with appressed hairs. Fruits known only in immature stage, ellipsoid, surface smooth; infructescence axis ca. 3 mm diam., fruit pedicels thickened to ca. 5 mm diam. below the fruit; fruit pedicels scarcely constricted at the apices.

*Flowering time.* September to November.

*Distribution.* Rio de Janeiro and Espírito Santo, Brazil (Fig. 15).

*Common names.* Canella tapinha (Kostermans, 1938), Canela-batata (*de Lima et al.* 3707).

*Selected specimens examined.* BRAZIL. **Rio de Janeiro:** Alto Macaé de Nova et Serra de Estrella, Oct.–Nov. (fl), *Glaziou* 20444 (C, K, NY).

*Beilschmiedia rigida* belongs to the *B. curvira-meae* group, but has some distinct cuticular characters, showing relatively thick, straight anticlinal walls (Nishida & Christophel, 1999). This species is distinguished by its opposite, obovate leaves, rounded leaf apices, long petioles, larger flowers, and thicker inflorescence rachises.



**23. *Beilschmiedia riparia*** Miranda, Anales Inst. Biol. Univ. Nac. México 24: 75. 1953. TYPE: Mexico. Chiapas: ca. 7 km SE of Tuxtla Gutiérrez, border of the stream of Cerro Hueco, ca. 700 m, 4 Feb. 1951 (fl), *Miranda 6872* (holotype, MEXU!; isotype, F!).

*Persea primatogena* L. O. Williams & A. R. Molina, Econ. Bot. 31: 319. 1977. TYPE: Nicaragua. Matagalpa: Cordillera Central de Nicaragua, finca Sta. María de Ostuma, 1300–1400 m, 30 Nov. 1973 (fr), *Williams & Molina 42575* (F!, EAP not seen).

Tree, to 40 m tall. Terminal buds pubescent with erect, straight to wavy or rarely curly hairs. Twigs terete, rarely compressed when young, relatively densely pubescent with erect, straight to wavy curly hairs, less densely pubescent or rarely glabrous when old. Leaves alternate, rarely subopposite; petioles 1–2 cm long, flat above, glabrous or pubescent with erect, straight to wavy hairs, densely pubescent when young, concolorous with twigs; blades chartaceous, elliptic, rarely ovate, sometimes asymmetric, 7–16.5 × 4–7.5 cm; base cuneate, rarely obtuse, not inrolled, apex acute to obtuse; upper leaf surface glabrous, lower leaf surface pubescent with erect, straight to wavy hairs when young, glabrous when old, or sometimes hairs remaining on the midrib and secondary veins even when old; lower leaf surface not or very rarely glaucous; midrib and secondary veins immersed above, raised below, secondary veins 8 to 13 pairs, tertiary veins not percurrent or rarely ± percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed (the pattern visible) above, slightly raised below. Inflorescences in axils of leaves, rarely clustered on the buds, 2–14 cm long, pubescent with erect, wavy to curly hairs, with 15–100 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–0.7 mm long, pedicels of the central flowers up to 1.5 (rarely 2) mm long. Flowers white to creamy 2–3 mm long, 2.3–3 mm diam.; tepals 6, equal, ovate to elliptic, ca. 2 mm long, 1.5 mm wide, pubescent with erect, slightly wavy hairs on both sides; stamens 9, outer six filaments 0.3–0.5 mm long, innermost three filaments ca. 0.7 mm long, filaments pubescent; anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and pubescent (very rarely glabrous), glands of the innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous to sparsely pubescent, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, 4 × 1.5 cm, surface smooth; fruit pedicels ca. 2 mm diam., scarcely

thickened below the fruit, pedicels constricted at the apices.

*Flowering time.* January to May.

*Distribution and habitat.* Southern Mexico, southern Honduras, and Nicaragua (Fig. 15); (480–)700–1500 m; along streams in semi-deciduous forests or mixed cloud forests.

*Common names.* Guaquemico, Aguacate de mico, Aguacatillo (*Bachem et al. 1000*), (Mexico); Aguacatillo colorado (*von Hagen & von Hagen 1257*) (Honduras); Aguacate de monte (*Standley 10857*) (Nicaragua).

*Selected specimens examined.* MEXICO. **Chiapas:** Municipio Villaflores, Depresion Central and Sierra Madre, Finca Ocotlan, 740 m, 21 Apr. 1989 (immature fr), *Bachem et al. 1000* (MO). **Guerrero:** Municipio Chilpancingo, Cañada Las Hamacas, path to Soyatepec, 750 m, 2 May 1988 (fl), *L. C. Rodríguez 374* (FCME, MO). **Oaxaca:** Municipio San Miguel Chimalapa, 2 km N to Col. Rodolfo Figueroa road to Díaz Ordaz and B. Juárez, 16°34'N, 94°12'W, ca. 1400 m, 28 Mar. 1984 (fl), *Wendt & Rico 4338* (MO). **Veracruz:** Misantla, June 1866 (fr), *M. Hahn s.n.* (P). HONDURAS. **Tegucigalpa:** locality unknown, ca. 840 m, 16 Dec. 1937 (sterile), *C. & W. von Hagen 1257* (NY). NICARAGUA. **Estelí:** entre Plan Helado y la laguna de Mirafior, El Zacatón, 13°14'N, 86°15'W, 1400 m, 30 June 1983 (immature fr), *Moreno 21657* (MEXU, MO). **Jinotega:** vicinity of Finca San Roque, sierra E of Jinotega, 1300–1500 m, 5 July 1947 (sterile), *Standley 10857* (F).

*Beilschmiedia riparia* belongs to the *B. costaricensis* group. This species is distinguished by the following characters: erect pubescence on the terminal buds and twigs, secondary veins raised below, a fine blade venation pattern, pubescent anthers, and elliptic fruits. To separate *B. riparia* from the similar *B. immersinervis*, see the discussion under the latter.

**24. *Beilschmiedia steyermarkii*** C. K. Allen, J. Arnold Arbor. 26: 417. 1945. TYPE: Guatemala. Alta Verapaz: S of Cubilagüitz, 300–400 m, 3 Mar. 1942 (fl), *Steyermark 44494* (holotype, F!).

Tree, to 27 m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, slightly angular when young, pubescent with erect, short wavy hairs to glabrous, less densely pubescent when older. Leaves alternate; petioles 1–1.7 cm long, flat to canaliculate above, glabrous to pubescent with erect, short curly hairs, concolorous with the twigs; blades coriaceous, elliptic to narrowly ovate, often asymmetric, 5–10 × 1.5–4 cm; base and apex acute, rarely apex obtuse, glabrous on both sides; lower leaf surface uncertain whether glaucous or not; midrib immersed above, raised below, second-



ary veins in 7 or 8 pairs, immersed above, slightly raised below, tertiary veins not percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above (sometimes the pattern visible above), slightly raised below. Inflorescences in axils of leaves, tending to cluster near the top of the branchlets, paniculate, 4–8 cm long, pubescent with erect short wavy hairs, with 25 to 65 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.4 mm long, ca. 2.5 mm diam.; tepals 6, equal, ovate to elliptical, ca. 1.5 × 1 mm, pubescent with erect wavy hairs outside, erect and wavy, or appressed hairs inside; stamens 9, filaments 0.3–0.6 mm long, pubescent, anthers 0.6–0.8 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost stamens globose, staminodia 3, sagittate, ca. 0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with erect wavy hairs, less densely pubescent to glabrous toward the bottom. Fruits unknown.

*Flowering time.* March.

*Distribution.* Guatemala (Fig. 15); 300–400 m.

*Additional specimen examined.* GUATEMALA. Los Arcos, 149 km of Cadenas Road, 22 Dec. 1969 (young fl), Contreras 9448 (C, F, MO).

*Beilschmiedia steyermarkii* is similar to *B. ovalis* in pubescence type, venation pattern, and floral structure but differs in its narrow leaves. Additionally, the two collections annotated herein are from 300–400 m altitude, which is a too low an elevation for *B. ovalis* (which typically occurs above 1800 m elevation).

*Beilschmiedia steyermarkii* also vegetatively resembles *B. immersinervis* (see the discussion under the latter).

As Allen (1945) reported, the type specimen of *B. steyermarkii* has few-flowered inflorescences. However, precise floral number is uncertain because the inflorescences are broken. The second specimen, collected after Allen's description, has inflorescences with relatively many (40 to 65) flowers.

**25. *Beilschmiedia stricta*** Kosterm., Rec. Trav. Bot. Néerl. 35: 863. 1938. TYPE: Brazil. Rio de Janeiro: G. Portella, Monte Sinai, 1935 (fl), Nunes 313 (holotype, U not seen; isotype, RB!).

Tree, height unknown. Terminal buds pubescent with appressed straight hairs. Twigs terete, younger

ones compressed, sparsely pubescent with appressed hairs, less densely pubescent to glabrous when older. Leaves opposite; petioles ca. 1 cm long, canaliculate to flat above, glabrous, slightly darker than branches; blades firmly chartaceous, elliptic, (5–)8–9 × 2.5–4 cm; base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides; lower leaf surface not glaucous; midrib immersed or impressed above, raised below, secondary veins 9 to 13 pairs, raised on both sides, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins raised on both sides. Inflorescences in axils of leaves, racemose, 1.5–2.5 cm long, pubescent with ± appressed hairs, with 5 to 10 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm diam.; tepals 6, almost equal, ovate, ca. 1.8 mm long, 1.2–1.5 mm wide, pubescent with appressed hairs outside, sparsely pubescent with appressed hairs or almost glabrous inside; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments ca. 0.5 mm long, pubescent, anthers ca. 1.1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of innermost three stamens globose; staminodia 3, sagittate, ca. 0.8 mm long; pistil 1.4–1.6 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Mature fruits unknown, young fruit ellipsoid, surface warty; young fruit pedicels not constricted at the apices.

*Distribution.* Rio de Janeiro, Brazil (Fig. 16).

*Beilschmiedia stricta* is known only from the type collection. It appears to be similar to *B. curviramea* and *B. fluminensis* in leaf shape and flower structure (see the discussion under these two species respectively).

**26. *Beilschmiedia taubertiana*** (Schwacke & Mez) Kosterm., Rec. Trav. Bot. Néerl. 35: 863. 1938. *Hufelandia taubertiana* Schwacke & Mez, Arb. Bot. Gart. Breslau 1: 108. 1892. TYPE: Brazil. Minas Gerais: Rio Novo, 1890 (fl & fr), Araujo 7047 (lectotype, designated by Kostermans (1938), B photo!; isolectotypes, P!, RB!).

Tree, height unknown. Terminal buds pubescent with erect, long straight hairs. Twigs terete, younger ones compressed, pubescent with erect, long straight or slightly wavy hairs, less densely pubescent when old. Leaves opposite; petioles 0.8–1 cm long, canaliculate above, pubescent with erect long



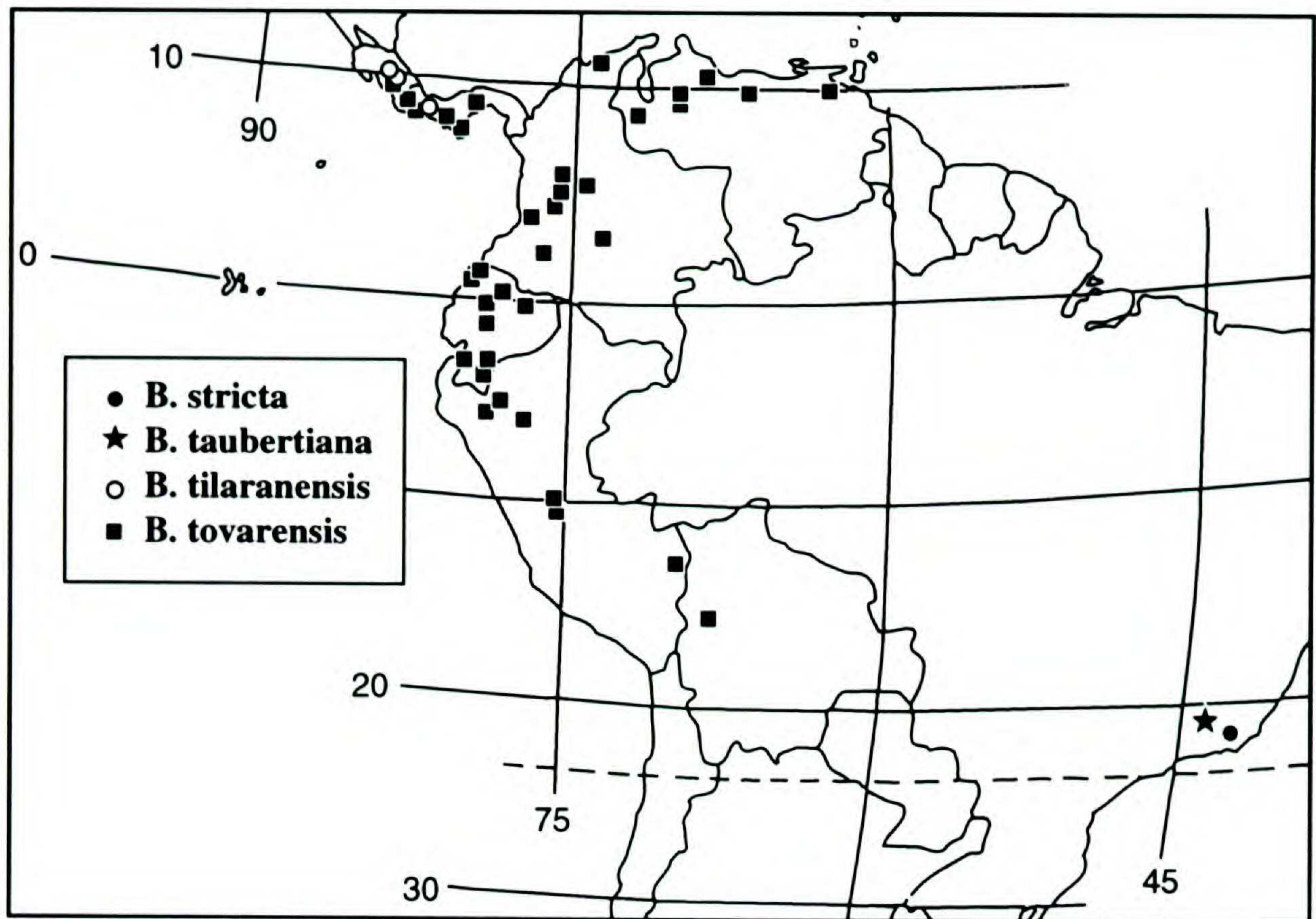


Figure 16. Representative distribution of *Beilschmiedia stricta*, *B. taubertiana*, *B. tilaranensis*, and *B. tovarensis*.

hairs, slightly discolored from twigs; blades firmly chartaceous, elliptic,  $10\text{--}14 \times 4\text{--}5$  cm; base obtuse to rounded, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface sparsely pubescent with erect, long straight to slightly wavy hairs; lower leaf surface not known whether glaucous or not; midrib immersed above, raised below, secondary veins 9 to 14 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, minor venation pattern coarse, areoles with branched free-ending veinlets inside, tertiaries and minor veins slightly raised on both sides. Inflorescences in axils of leaves, racemose, ca. 1.5 cm long, pubescent with erect long hairs, with ca. 5 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 4 mm long. Flowers ca. 3 mm long, ca. 3 mm diam.; tepals 6, equal, ovate, 1.9–2 mm long, 1.3–1.5 mm wide, pubescent with erect long wavy hairs outside, sparsely pubescent with appressed to erect hairs inside; stamens 9, outer 6 filaments ca. 0.3 mm long, innermost 3 filaments ca. 0.4 mm long, filaments pubescent, outer six anthers 1.2–1.3 mm long, innermost anthers 0.9–1.1 mm long, 2-celled, anther apices obtuse to truncate and pubescent, glands of the innermost 3 stamens globose; staminodia 3, sagittate, ca. 0.6 mm long; pistil ca. 1.2 mm long, glabrous, ovary shorter than and gradually narrowed into the style; receptacle densely pubescent with erect hairs. Fruits ellipsoid, ca. 5

$\times 3$  cm, surface warty; infructescence axis ca. 3 mm diam., fruit pedicels thickened to ca. 5 mm diam. below the fruit, not constricted at the apices.

*Distribution.* Southern Minas Gerais, Brazil (Fig. 16).

*Additional specimen examined.* BRAZIL. **Minas Gerais:** Rio Novo, 1889 (sterile), Araujo 5 (RB).

Among southeastern Brazilian species, *Beilschmiedia taubertiana* is easily distinguished by its erect, long straight pubescence on terminal buds and twigs, and by the lower leaf surfaces sparsely and similarly pubescent.

**27. *Beilschmiedia tilaranensis*** Sa. Nishida, sp. nov. TYPE: Costa Rica. Guanacaste: Cantón de Tilarán, Cordillera de Tilarán, Las Nubes de Río Chiquito, Mt. Olivo,  $10^{\circ}21'00''\text{N}$ ,  $84^{\circ}51'00''\text{W}$ , 1450 m, 29 Jan. 1992 (fr), *Guindon & Brenes 40* (holotype, MO!; isotypes, CR!, INB!, USJ!). Figure 17.

Haec species *Beilschmiediae ovali* affinis, sed ab ea foliis obovatis, venis tertiariis valde percurrentibus atque fructu ellipsoideo differt, necnon quam ea in altitudinibus inferioribus habitat.

Tree, to 20 m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete, angular when young, densely pubescent with erect short curly hairs, less dense when old. Leaves alternate; peti-



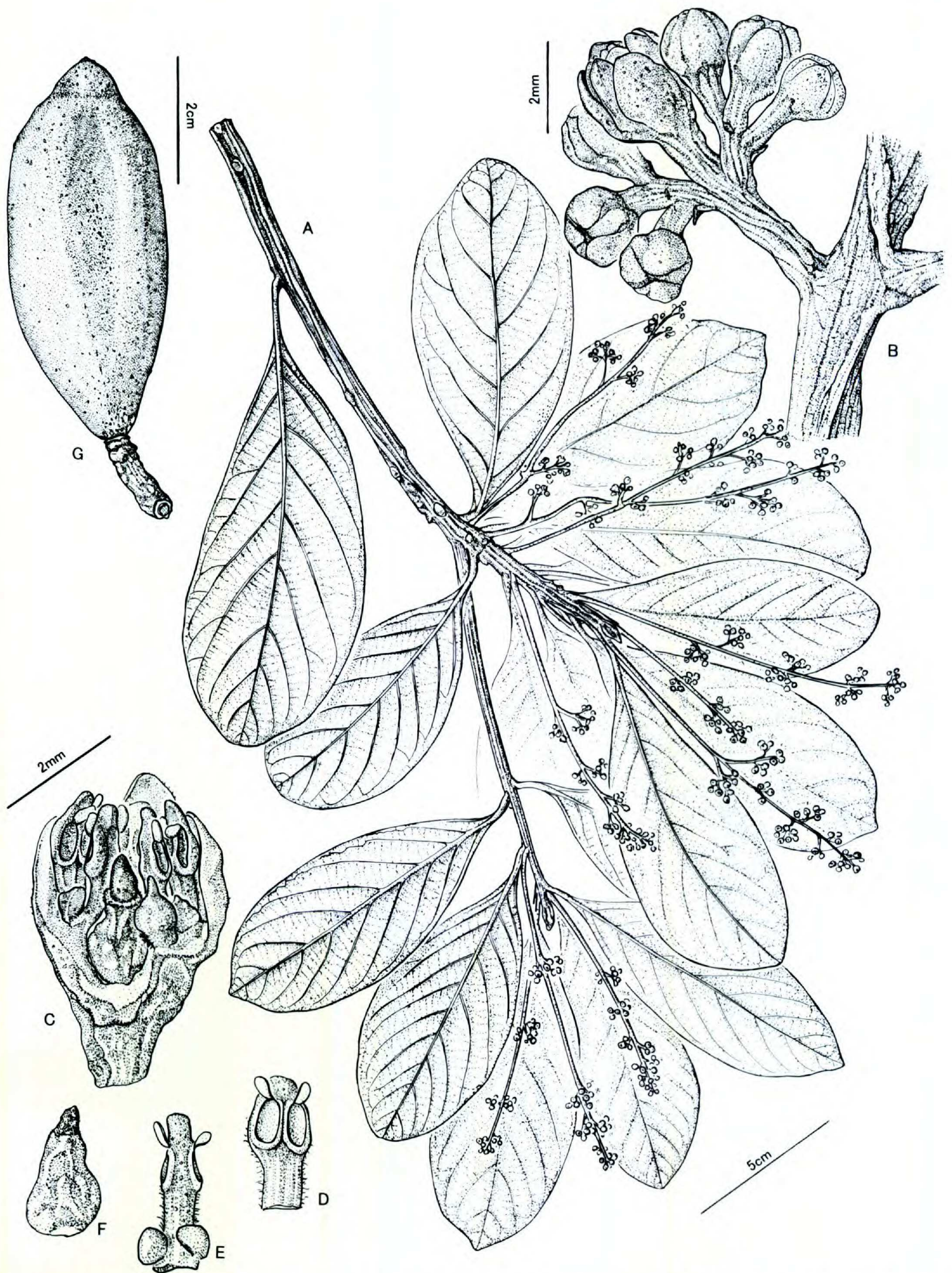


Figure 17. *Beilschmiedia tilaranensis* (A–F, Haber 11092, G, Guindon 40). —A. Flowering branch. —B. Part of inflorescence. —C. Lateral section through flower, showing stamens, two glands, staminode, and pistil. —D. Stamen of whorl I/II, ventral view. —E. Stamen of whorl III with two glands, dorsal view. —F. Pistil. —G. Fruit.



oles 1–2 cm long, almost flat above, sparsely pubescent with erect short curly hairs, concolorous with twigs; blades coriaceous, obovate, rarely elliptic, 6–13 × 4–7 cm; base cuneate, not inrolled, apex obtuse; leaf surface glabrous on both sides; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 7 to 11 pairs, almost immersed, rarely impressed above, raised below, tertiary veins percurrent, minor venation pattern fine, areoles without free-ending veinlets inside, tertiaries and minor veins immersed above, raised below. Inflorescences in axils of leaves, paniculate, 5–12 cm long, sparsely pubescent with erect short curly hairs or almost glabrous, with 20 to 30 flowers per inflorescence; floral pedicels of the lateral divisions 0.5–1 mm long, pedicels of the central flowers up to 2 mm long. Flowers creamy, ca. 2.3 mm long, ca. 2.6 mm diam.; tepals 6, equal, ovate, ca. 1.5 mm long, ca. 1.2 mm wide, sparsely pubescent with erect hairs on both sides; stamens 9, filaments 0.4–0.8 mm long, pubescent; anthers ca. 1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose; staminodia 3, deltoid, ca. 0.7 mm long; pistil ca. 1.5 mm long, glabrous, ovary as long as the style or longer than and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Fruits ellipsoid or obovoid, black, 5.5–6.5 × 2–2.5 cm, surface smooth; infructescence axis 3–4 mm diam., fruit pedicels thickened to 4–6 mm diam. below the fruit, not apically constricted.

*Flowering time.* April.

*Distribution and habitat.* Costa Rica and western Panama (Fig. 16); 1100–1580 m; premontane forest.

*Paratypes.* COSTA RICA. **Alajuela:** Cerros de la Palma de San Ramón, 1300–1500 m, 24 Jan. 1984 (fr), *J. Gómez L. 9800* (CR, F). **Guanacaste:** Parque Nacional Guanacaste, Estación Cacao, Liberia, 10°55'45"N, 85°28'15"W, 1100 m, 11 Dec. 1990 (immature fr), *Chávez 443* (MO); 1 km N of La Cruz, 10°21'N, 84°50'W, ca. 1480 m, 10 Mar. 1996 (immature fr), *Yasuda et al. 1313* (INB, MO). **Puntarenas:** Cantón de Tilarán 4–5 km NW Monteverde, 2–4 km W of Santa Elena between road to Cañitas and upper road to Las Nubes, 10°20'N, 84°49'W, 1400–1500 m, 11 Apr. 1992 (fl), *Haber et al. 11092* (INB, MO); Las Alturas de Coto Brus, 8°54'N, 82°50'W, 1150–1250 m, 20 Mar. 1987 (fr), *Burger et al. 12184* (F, MO, NY); Estación Biológica Las Alturas, 8°57'15"N, 83°50'10"W, 1580 m, 7 Mar. 1996 (sterile), *Yasuda et al. 1307* (INB). PANAMA. **Coclé:** sawmill above El Copé Pacific slope, ca. 1100 m, 9 Mar. 1979 (fr), *Hammel 6286* (MO).

Burger and van der Werff (1990) reported that a few collections in *Beilschmiedia ovalis* had atypically

obovate leaves and commented that these might belong to an undescribed species. Since then, additional specimens with pubescence and leaf texture similar to *B. ovalis* but with these obovate leaves have been collected from elevations lower than where *B. ovalis* occurs. These collections consistently have ellipsoid fruits, also different from the spherical fruits of *B. ovalis*. Obovate leaves, ellipsoid fruits, and a lower-elevational habitat clearly distinguish these collections as a new species. In addition, *B. tilaranensis* has leaf tertiary veins conspicuously percurrent, a condition rarely seen in *B. ovalis*.

**28. *Beilschmiedia towarensis*** (Meisn.) Sa. Nishida, comb. nov. Basionym: *Hufelandia towarensis* Meisn., in DC., Prodr. 15 (1): 65. 1864. SYNTYPES: Colombia. Locality unknown, *Karsten 88* (B photo!). Venezuela. Mérida: Tovar, ca. 1920 m, 28 Aug. 1854 (fl), *Fendler 1094* (NY!).

*Aniba pseudo-coto* (Rusby) Kosterm., Rec. Trav. Bot. Néerl. 35: 872. 1938. *Ocotea pseudo-coto* Rusby, Bull. Torrey Bot. Club 49: 261. 1922. TYPE: Bolivia. La Paz: mountains S of Huachi, near the Cochabamba River, 750–900 m, 9 Sep. 1921 (young fl), *White 1051* (lectotype, designated by Kostermans (1938), NY photo!; isolectotypes, AFS not seen, C!, G-DEL not seen, GH not seen, K!, US photo!).

Tree, to 40 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly angular when young, pubescent with appressed straight hairs, less densely pubescent when older. Leaves alternate; petioles 0.5–4.2 cm long, flat to canaliculate above, glabrous or pubescent with appressed straight hairs, concolorous with twigs; blades coriaceous to firmly chartaceous, ovate to broadly elliptic, rarely broadly oblanceolate, (5–)8–20(–28) × 4–14 cm; base cordate to obtuse, rarely cuneate, not inrolled, apex acuminate, rarely acute; upper leaf surface glabrous, lower leaf surface pubescent with appressed short straight hairs; lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 5 to 11 pairs, immersed or slightly raised above, raised below, tertiary veins percurrent, minor venation pattern fine, areoles lacking free-ending veinlets inside, tertiaries and minor veins immersed above (the fine pattern sometimes slightly visible), almost immersed below (the pattern visible). Inflorescences in axils of leaves near the terminal buds, sometimes in axils of cataphylls below leaves near tips of the twigs, paniculate, 4–16(–23) cm long, pubescent with short, appressed to erect hairs, with 30 to 100 flowers per inflorescence; floral pedicels of the lateral



divisions 0.5–1.5 mm long, pedicels of the central flowers up to 3 mm long. Flowers yellowish white, 2–3 mm long, 2–3 mm diam.; tepals 6, equal, ovate to elliptic, 1.3–2 mm long, 1–1.5 mm wide, pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3–0.4 mm long, innermost three filaments 0.4–0.7 mm long, filaments pubescent, anthers 0.7–1 mm long, 2-celled, anther apices obtuse to truncate and glabrous, glands of the innermost three stamens globose, staminodia 3, sagittate, ca. 0.7 mm long; pistil ca. 1.3 mm long, sparsely pubescent to glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely pubescent toward the bottom. Fruit ellipsoid, purple-black, 2.5–3.5 × 1.5–2 cm, surface smooth; infructescence axis 2–3 mm diam., fruit pedicels scarcely thickened below fruits, constricted or not constricted at the apices.

*Flowering time.* July to March.

*Distribution and habitat.* Southern Costa Rica, Panama, northern Venezuela, Colombia, Ecuador, Peru, and western Bolivia (Fig. 16); (1–)500–2200(–3000) m; premontane wet forest to cloud forest.

*Common names.* Aguacatillo (*Figueiras 8401*) (Colombia); Aguacatillo (*Alvarez et al. 625*), Aguacatillo de montaña (*Little, Jr. 6657*) (Ecuador); Roble palta (*van der Werff et al. 8329*), Palta moena, Moena (*Albán 4085*) (Peru).

*Selected specimens examined.* COSTA RICA. **Heredia:** Volcán Barba, 4 Mar. 1983 (fr), *Peralta s.n.* (CR). **Puntarenas:** Cantón of Golfito Jiménez, Dos Brazos de Río Tigre, enroute between the ravines, Cerro Mueller and Cerro Rincón, 8°30'35"N, 83°28'15"W, 782 m, 25 Nov. 1990 (fl), *Herrera 4643* (MO). **San José:** Cantón Pérez Zeledón San Isidro de El General, El Pilar de Cajón, plots of Las Brisas de Cajón, 9°22'50"N, 83°36'45"W, 600 m, 16 Apr. 1992 (immature fr), *Zamora et al. 1819* (MO). PANAMA. **Barro Colorado Isl.:** Lutz Trail cut-off behind Animal house, 23 May 1968 (fr), *Croat 5813* (F, MO, NY). **Canal Zone:** Pipeline Road, 6 km N of Gamboa, 3 Dec. 1971 (sterile), *Gentry 2829* (MO). **Chiriquí:** road from Volcán to Río Serano, road that turns E 7.2 km from Río Serano, 1.2 km along the side road, 29 June 1977 (fr), *Folson 4040* (MO). **Los Santos:** Coabal, Progrese, W slope above Río Cobachén, 200 m, 19 Apr. 1968 (immature fr), *Holdridge 6209* (MO). **Panamá:** Cerro Campana, 900 m, 13 Apr. 1967 (fl), *Duke 10749* (MO). **Veraguas:** District of Montijo, Cerro Hoya Nacional Park, ca. 900 m, 7 Mar. 1993 (immature fr), *N. Rivera 324* (MO). VENEZUELA. **Aragua:** Henri Pittier National Park, 31 Aug. 1990 (fl), *Cardozo et al. 1549* (MO). **Mérida:** La Trampa, highway San Juan–Azulita, 2500 m, 2 Feb. 1987 (sterile), *van der Werff et al. 8766* (MO). **Monagas:** Distrito Caripe, forest adjacent to the cave of El Guácharo, 1000–1100 m, 16 July 1985 (sterile), *Lau 16* (MO). **Portuguesa:** Distrito Sucre, Concepción division, 9°18'N, 70°06'W, 1700 m, 24 Oct. 1985 (immature fr), *van der Werff et al. 7575* (MO).

**Trujillo:** Carache District, road between La Playa (9°37'N, 70°8'W), SW of Carache, & Potreritos de Cendé (9°32'N, 70°8'W), ca. 10–14 km from La Playa, 2200 m, 11 May 1988 (immature fr), *Dorr et al. 5114* (MO). **Yaracuy:** 7–10 km N of Salom, El Amparo near Candelaria, 1100–1300 m, 27–30 Dec. 1972 (young fl), *Steyermark & Espinoza 106806* (NY). COLOMBIA. **Antioquia:** Municipio of San Luís, canyon of Río Claro, S sector, right edge, 5°53'N, 74°39'W, 325–450 m, 29 Jan. 1984 (immature fr), *Cogolla 1285* (MO). **Boyaca:** 100 m NW of Bogotá, extreme W part of Department Boyaca, region of Mt. Chapon, ca. 1080 m, 23 July 1932 (immature fr), *Laurance 353* (BM, F, K, NY, U). **Caldas:** Municipio Risaralda, Quebrada Chovarquí, 1140 m, 14 Nov. 1992 (immature fr), *Vargas 754* (MO). **Cauca:** Tierra Odentro, around Huila, Indian village in Río Paez Valley, 1600–1900 m, Jan. 1906 (immature fr), *Pittier 1286* (NY). **Magdalena:** region near Santa Marta, 2250 m, 2 Mar. 1932 (sterile), *Espina & Giacometto A170* (NY). **Meta:** Sierra de la Macarena, Caño Entrada, 550 m, 13 Jan. 1950 (immature fr), *Philipson et al. 2094* (NY). **Valle:** Cordillera Occidental, valley of Río Cali, suburb of Peffas Blancas, 23 Jan. 1963 (fl), *Figueiras 8401* (US). ECUADOR. **Bolívar:** Road Echandia–Guaranda, 2000 m, 17 July 1991 (fl), *van der Werff et al. 12406* (MO). **Esmeraldas:** Cantón San Lorenzo, Parroquia Alto Tambo, Sector El Cristal, 01°30'N, 78°30'W, 600 m, 13 Apr. 1992 (fr), *Tipaz et al. 792* (MO). **Imbabura:** Cotacachi, Hda. La Florida, 0°23'S, 78°28'W, 1900–2500 m, 28 Aug. 1992 (sterile), *Alvarez et al. 625* (MO). **Morona-Santiago:** 11.7 km SW of Taisha, 2°32'S, 77°44'W, 11–15 Sep. 1976 (sterile), *Ortega 138* (US). **Napo:** Canton Quijos, Chaco, road to Cayambe-Coca Reserve, Río San Juan Chico, following to Río Oyacachi, 00°17'S, 77°03'W, 1750 m, 12 Jan. 1992 (young fl & fr), *Palacios et al. 9554* (MO). **El Oro:** 15 km S of Piedras, Ingenio farm, 700–1000 m, 20 June 1943 (immature fr), *Little, Jr. 6657* (NY, US). **Pichincha:** along new road Nanegal–Mindó, 1500–1800 m, 2 Mar. 1994 (young fl), *van der Werff et al. 13377* (MO). PERU. **Amazonas:** Luya Province, Jaípe, Fundo El Paraíso, 1690 m, 31 May 1989 (immature fr), *Díaz & Campos 3587* (MO). **Cajamarca:** Provincia Jaen, Colasay, hills NW of town, 5°58'S, 79°03'W, 2100 m, 21 Feb. 1985 (fr), *Stein & Todzia 2231* (MO, NY). **Huánuco:** Provincia Pachitea, Honoria, Caserío Leoncio, Aug. 9, 1963 (fl), *R. Lao M. 66* (F, NY, US). **Madre de Dios:** Tambopata Tourist Camp, junction of Ríos la Torre and Tambopata, 12°50'S, 69°17'W, 260 m, 6 June 1986 (immature fr), *Gentry & Nuñez 54196* (MO). **Pasco:** Provincia Oxapampa, 1800 m, 3 Mar. 1986 (immature fr), *van der Werff et al. 8329* (MO). **San Martín:** Provincia Moyobamba, Soritor, 680 m, 23 July 1986 (sterile), *Albán 4085* (F). BOLIVIA. **La Paz:** Provincia Larecaja, Copacabana (ca. 10 km S of Mapiri), 850–950 m, 8 Oct.–15 Nov. 1939 (fl), *Krukoff 11235* (F, MO, U).

*Beilschmiedia towarensis* belongs to the *B. costaricensis* group. It is distinguished by the following characters: appressed pubescence on the terminal buds and twigs, alternate leaves, lower leaf surfaces pubescent with appressed hairs, rounded areoles, glabrous anthers, and ellipsoid fruits. This species is broadly based on two specimen groups. One group has ovaries that are pubescent, whereas the second group has ovaries that are glabrous. Those



with pubescent ovaries tend to have shorter petioles and coriaceous, ovate to broadly elliptic leaves with fruit pedicels not apically constricted. Those with glabrous ovaries tend to have longer petioles, rigid chartaceous, elliptic leaves, and fruit pedicels apically constricted. Careful survey of leaf morphology revealed many intermediate collections, and a clear separation between the two groups cannot be made for petiole length and leaf size. Additionally, there are some exceptions in the groups indicated by the pubescence of ovaries. Within the same collections, duplicates may have short petioles, ovate leaves, and glabrous ovaries, or long petioles, elliptic leaves, and pubescent ovaries. Both groups occur from Venezuela to Bolivia, although glabrous ovaries are more often observed in specimens from Costa Rica and Panama. This species has an unusually wide range of morphology and geographic distribution, but the two groups are retained together in this species because of the existence of many intermediate specimens.

Specimens with glabrous ovaries have sometimes been identified as *B. pendula*, but can usually be distinguished from it by the very fine areoles lacking free-ending veinlets, longer (1.5–3.5 cm long) petioles, and larger (8–20 × 4–14 cm) leaves.

#### IMPERFECTLY KNOWN SPECIES

*Beilschmiedia sulcata* (Ruiz & Pav.) Kosterm., *Revueil. Trav. Bot. Néerl.* 35: 850. 1938. *Laurus sulcata* Ruiz & Pav., *Fl. Peruv.* 4: 356. 1804. *Hufelandia sulcata* (Ruiz & Pav.) Nees, *Linnaea* 21: 494. 1848. *Persea sulcata* (Ruiz & Pav.) Meisn., in DC., *Prodr.* 15(1): 54. 1864. TYPE: Peru. Muña, (immature? fr), *Ruiz s.n.* (lectotype, designated by Kostermans (1938), MA photo!; isolectotypes, B not seen, BM!, F!, G-BOIS not seen).

In Ruiz and Pavon's (1804) illustration of *Laurus sulcata* in *Flora Peruviana*, the anthers are drawn as having 4 cells. However, there are no flowers in the holotype seen by Velayos (pers. comm.) or any isotypes I have seen. It is unknown whether the illustration is correct and this is a species of *Beilschmiedia* with 4-celled anthers, or if the illustration is erroneous. Thus far no fertile specimen has been located that corresponds to the type or illustration.

*Beilschmiedia zapoteoides* (Lundell) Kosterm., *Reinwardtia* 6: 156. 1962. *Endlicheria zapoteoides* Lundell, *Wrightia* 1: 145. 1946. TYPE: Mexico. Chiapas: Cascada near Siltepec, in advanced forest, 1600 m, 1 Mar. 1945 (fl &

fr), *Matuda* 5153 (holotype, TEX!; isotypes, MO!, US!).

The type collection of *Beilschmiedia zapoteoides* approaches *B. hondurensis*, but it is distinguished from the latter by its having relatively longer floral pedicels (ca. 2 mm long in the lateral divisions) and more or less spherical fruits. However, the type collection of *B. zapoteoides* appears to be abnormal: its leaves are diseased, and the number of cells in the stamens of the third whorls is variable, from two to zero.

#### EXCLUDED SPECIES

- Beilschmiedia brasiliensis* (Kosterm.) Kosterm. = *Anaueria brasiliensis* Kosterm.  
*Beilschmiedia cuneata* (Meisn.) Kosterm. = *Persea cuneata* Meisn.  
*Beilschmiedia durifolia* (Mez) Kosterm. = *Persea durifolia* Mez  
*Beilschmiedia inaequalis* (A. C. Sm.) Kosterm. = *Caryodaphnopsis inaequalis* (A. C. Sm.) van der Werff & H. G. Richter  
*Beilschmiedia lundelliana* Lasser = *Persea cuneata* Meisn.  
*Beilschmiedia sphaerocarpa* H. Winkl. Affinity uncertain.

#### Literature Cited

- Allen, C. K. 1945. Studies in the Lauraceae, VI: Preliminary survey of the Mexican and Central American species. *J. Arnold Arbor.* 26: 280–434.  
 Blake, S. F. 1919. The anay, a new edible-fruited relative of the avocado. *J. Wash. Acad. Sci.* 9: 457–462.  
 Burger, W. C. & H. van der Werff. 1990. Flora Costaricensis, Family #80, Lauraceae. *Fieldiana Bot. N. S.* 23: 1–129.  
 Christophel, D. C. & A. Rowett. 1996. Leaf and Cuticle Atlas of Australian Leafy Lauraceae. Australian Biological Resources Study, Canberra.  
 ———, R. Kerrigan & A. I. Rowett. 1996. The use of cuticular features in the taxonomy of the Lauraceae. *Ann. Missouri Bot. Gard.* 83: 419–432.  
 Gay, C. 1849–1852. *Historia Fisica y Politica de Chile, Botánica*, Vol. 5. E. Thunot y C., Paris.  
 Hemsley, W. B. 1882. *Biologia Centrali-Americana, Botany*, Vol. 3. Published for the editors by R. H. Porter and Dulau, London.  
 Heusser, C. J. 1971. *Pollen and Spores of Chile*. Univ. Arizona Press, Tucson.  
 Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.* 60: 17–33.  
 ———. 1979. A revised classification of the architecture of dicotyledonous leaves. Pp. 25–39 in C. R. Metcalfe & L. Chalk (editors), *Anatomy of the Dicotyledons*, 2nd ed., Vol. 1. Clarendon Press, Oxford.  
 Hutchinson, J. 1964. *The Genera of Flowering Plants (Dicotyledonae)*, Vol. 1. Oxford Univ. Press, London.  
 Hyland, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*). *Austral. Syst. Bot.* 2: 135–367.



- Kostermans, A. J. G. H. 1938. Revision of the Lauraceae V, A. Monograph of the genera: *Anaueria*, *Beilschmiedia* (American species) and *Aniba*. Recueil. Trav. Bot. Néerl. 35: 834–928.
- . 1952. A historical survey of Lauraceae. J. Sci. Res. (Jakarta) 1: 141–159.
- . 1957. Lauraceae. Reinwardtia 4: 193–256.
- Kuntze, C. E. O. 1891. Revisio Generum Plantarum, Vol. 2. Arthur Felix, Leipzig.
- Lorea-Hernández, F. G. 1995. A new species of *Beilschmiedia* (Lauraceae) from Guerrero, Mexico. Novon 5: 45–47.
- Meisner, C. F. 1864. Lauraceae. Pp. 1–260 in A. P. De Candolle, Prodrum Systematis Naturalis Regni Vegetabilis, Vol. 15. Treuttel & Würtz, Paris.
- Mez, C. 1889. Lauraceae Americanae. Jahrb. Königl. Bot. Gart. Berlin 5: 1–556.
- Nees von Esenbeck, C. G. D. 1831. Laurinae Indiae Orientalis. Pp. 58–76 in N. Wallich, Plantae Asiaticae Rariores, Vol. 2. Treuttel & Würtz, London.
- . 1833. Plantarum Laurinarum Secundum Affinitates Naturales Expositio. (No publisher indicated) Breslau.
- . 1836. Systema Laurinarum. Veit, Berlin.
- Nishida, S. & D. C. Christophel. 1999. Leaf anatomy of *Beilschmiedia* (Lauraceae) in the Neotropics. Nature and Human Activities 4. In press.
- Richter, H. G. 1981. Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderb. Naturwiss. Vereins, Hamburg, 5: 1–148.
- Ruiz, H. & J. A. Pavón. 1804 (preprint). Flora Peruviana, et Chilensis, Vol. 4. Later distributed by O. Rich.
- Werff, H. van der. 1995. Two new species of Lauraceae from central French Guiana. Brittonia 47: 372–375.
- & H. G. Richter. 1996. Toward an improved classification of Lauraceae. Ann. Missouri Bot. Gard. 83: 409–418.
- Wheelwright, N. T. 1986. A seven-year study of individual variation in fruit production in tropical bird-dispersed tree species in the family Lauraceae. Pp. 19–35 in A. Estrada & T. H. Fleming (editors), Frugivores and Seed Dispersal. Dr. W. Junk, Dordrecht.
- . 1995. Four constraints on coevolution between fruit-eating birds and fruiting plants: A tropical history. Acta Cong. Int. Ornith. 19: 827–845.
- , W. A. Haber, K. G. Murray & C. Guindon. 1984. Tropical fruit-eating birds and their food plants: A survey of a Costa Rican lower montane forest. Biotropica 16: 173–192.
16. *Beilschmiedia manantlanensis* Cuevas & Cochrane
17. *Beilschmiedia mexicana* (Mez) Kosterm.
18. *Beilschmiedia miersii* (Gay) Kosterm.
19. *Beilschmiedia ovalioides* Sa. Nishida
20. *Beilschmiedia ovalis* (S. F. Blake) C. K. Allen
21. *Beilschmiedia pendula* (Sw.) Hemsl.
22. *Beilschmiedia rigida* (Mez) Kosterm.
23. *Beilschmiedia riparia* Miranda
24. *Beilschmiedia steyermarkii* C. K. Allen
25. *Beilschmiedia stricta* Kosterm.
26. *Beilschmiedia taubertiana* (Schwacke & Mez) Kosterm.
27. *Beilschmiedia tilaranensis* Sa. Nishida
28. *Beilschmiedia towarensis* (Meisn.) Sa. Nishida

INDEX TO EXSCICCATAE

Examined specimens are listed alphabetically by collector, followed by collection numbers (and herbarium of deposit if anonymous); the species is indicated by a number in parentheses corresponding to the number in the List of Species.

Abbot, W. L. 2529 (21). Aguilar, R. 1308 (1); 1404 (1); 3346 (1). Aguilar, R. & R. Evans 4073 (21). Albán C., J. 4085 (28); 4095 (28); 4142 (28). Alfaro, E. 82 (7). Allen, C. K. 17 (7). Allen, C. K. & L. R. Terrán 25 (14). Allen, P. H. 3490 (20). Almeda, F. et al. 5639 (1). Alvarado, C. 126 (7). Alvarez, A. et al. 625 (28). Anonymous (INB 210) (BM, BR, F, MO, NY) (7); (INB 227) (CR, F, MO) (6); 438 (US) (17); 3261 (K) (8); (MO, NY) (5); (BM) (18); (BM) (21). Araujo 5 (26); 7047 (26). Atwell, C. & S. Moestl 2 (21). Augusto, B. 1569 (21). Aulestia 3494 (7). Auleuis s.n. (10).

B. T. 401 (28). Bachem C., U. et al. 1000 (23). Barbour, W. B. 1019 (21). Beard, J. S. 409 (21); 438 (21). Beard, P. 636 (21); 1454 (21). Bello C., E. 303 (7); 434 (6); 560 (7); 580 (6); 641 (7); 1914 (7); 2112 (7); 3212 (7); 3477 (7). Bello C., E. & E. Cruz 4882 (7). Bello C., E. & C. Méndez 2633 (7). Bello C., E. et al. 2779 (6); 4017 (27). Beltrán, W. 39 (7). Benalcazar, C. & F. C. Silva 19 (7); 59 (7). Benavides, O. de 6734 (28); 8964 (7). Berg, K. S. 46 (1). Bernardi, A. L. 6458 (28); 7452 (1); 10954 (14); 10955 (14); s.n. (6256?) (7). Bertero 4 (5); 760 (5); 1078 (18); s.n. (5). Betancur, J. et al. 1066 (28). Binot, M. 81 (4). Blanco, C. 27 (8). Blum, K. E. & J. Dwyer 2624 (7). Boelcke, O. 6466 (18). Bonifaz, C. & X. Cornejo 3091 (1). Bosque, C. 22 (28). Box, H. E. 1843 (21). Brade 18642 (10). Breedlove, D. E. 10040 (23); 56219 (17). Breedlove, D. E. & A. R. Smith 21817 (12); 31417 (12); 49052 (12). Brenes, A. M. 6214 (6); 6605 (7). Bridge 506 (18). Brigada Dioscoreas 279 (2); 392 (2). Brittan, N. 1472 (1). Britton, N. L. 660 (21); 3691 (21). Britton, N. L. & E. G. Britton 7364 (21). Britton, N. L. & J. F. Cowell 634 (21). Britton, N. L. & P. Wilson 5320 (21). Burger, W. et al. 12088 (7); 12178 (28); 12189 (28).

Cabrera R., I. 5252 (14). Caley, G. s.n. (8). Callejas, R. et al. 8368 (7). Campos 2951 (7); 3110 (28). Cardozo, A. et al. 1549 (28); 1563 (28). Carranza 653 (17); 832 (17). Castañeda, R. R. 2820 (21). Cedillo T., R. & D. Lorence 2372 (19). Cedillo T., R. et al. 822 (23); 828 (23). Celestino M., J. 1442 (28). Cerón M., C. E. 1662 (21). Chávez, C. 32 (7); 216 (6); 233 (7); 333 (6); 443 (27); 473 (7); 490 (7); 491 (1); 545 (6); 563 (6). Clark, J. L. & N. Pitman 248 (1). Clark, J. L. & Y. Troya 653 (1). Clark, J. L. & C. Watt 850 (1). Clark, J. L. et al. 1695 (1); 2541 (1); 2943 (1); 3763 (1). Cogolla, A. 1285 (28). Constantino, D. 19914 (4). Contreras, E. 9448 (24). Correa A., M. D. &

LIST OF SPECIES

1. *Beilschmiedia alloiophylla* (Rusby) Kosterm.
2. *Beilschmiedia anay* (S. F. Blake) Kosterm.
3. *Beilschmiedia angustielliptica* Lorea-Hern.
4. *Beilschmiedia angustifolia* Kosterm.
5. *Beilschmiedia berteroana* (Gay) Kosterm.
6. *Beilschmiedia brenesii* C. K. Allen
7. *Beilschmiedia costaricensis* (Mez & Pittier) C. K. Allen
8. *Beilschmiedia curviramea* (Meisn.) Kosterm.
9. *Beilschmiedia emarginata* (Meisn.) Kosterm.
10. *Beilschmiedia fluminensis* Kosterm.
11. *Beilschmiedia hexanthera* van der Werff
12. *Beilschmiedia hondurensis* Kosterm.
13. *Beilschmiedia immersinervis* Sa. Nishida
14. *Beilschmiedia latifolia* (Nees) Sa. Nishida
15. *Beilschmiedia linharensis* Sa. Nishida & van der Werff



- E. Montenegro 10408 (21); 11039 (21); 11164 (21). Croat, T. B. 5813 (28); 7034 (28); 8459 (28); 12659 A (28); 12928 (28); 14063 (28); 70684 (7); 70747 (7). Croat, T. B. & D. P. Hannon 64900 (17). de la Cruz, J. S. 1655 (8); 2249 (8); 2379 (8); 2725 (8). Cuatrecasas, J. 14876 (7); 14299 (28); 15193 (7); 15581 (7); 15619 (1); 18414 (28); 21747 (28). Cuatrecasas, J. & R. Romero-Castañeda 25413 (7). Cuatrecasas, J. et al. 29000 (14). Cuevas G., R. et al. 4076 (16).
- Davidse, G. 24222 (28). Davidse, G. & G. Herrera Ch. 29213 (7). Davidse, G. et al. 28226 (28). Dayton, W. A. 3123 (21). Devia A., W. 917 (7); 939 (7); 1050 (7); 1078 (7); 1079 (7). Devia A., W. et al. 2290 (28). Diar 112 (18). Díaz S., C. 2088 (7). Díaz S., C. & S. Baldeón 2464 (7). Díaz S., C. & J. Campos 3587 (28); 3714 (14); 3723 (14). Díaz S., C. et al. 3195 (7); 4355 (28); 4611 (28); 8739 (28). Dik, A. 626 (21). Dixon, R. G. 21265 (1). Dodson, C. H. & A. Gentry 6489 (1); 9906 (1). Dorr, L. J. et al. 5114 (28); 5117 (28). Dryer, V. J. 939 (7); 1081 (7); 1179 (7); 1334 (7). Duarte, A. P. 5007 (10). Duerto, P. 1 (14). Duke, J. A. 10749 (28). Duque 39 (28). Duss, P. 222 (21); 3863 (21); 4014 (= 4006) (21); 4096 (21). Dwyer, J. D. 2054 (7).
- Eggers 2087 (21). Eggers & C. Rensh 5434 (21). Ekman, E. L. H1950 (21); 5009 (21); 6402 (21); H14565 (21); 14826 (21). Enriquez 7568 (23). Espina & Giacometto A170 (28). Espinoza, R. 45 (6); 669 (6).
- Farias, G. L. 243 (15). Fendler 1094 (28). Fernández, A. 449 (6). Figueiras, L. 8401 (28). Folli, D. A. 409 (15); 2033 (15). Folsom, J. P. 4040 (28). Foster, R. B. 2053 (28). Foster, R. B. & I. Bokor 9460 (28). Freire 21 (14). Fuentes, P. M. 1617 (21). Fuentes, Z. & E. Fuentes 466 (6). Fuentes, Z. et al. 251 (6).
- Gallardo H., C. et al. 1007 (19). Gamboa, B. 84 (6). García, D. 362 (6). Garcia, R. & S. Peláez 952 (21). Garganta, de 680 (14). Gay, M. C. 236 (18); s.n. (5). Gentle, P. H. 7292 (12). Gentry, A. 2829 (28); 50932 (21). Gentry, A. & M. Fallen 17136 (7). Gentry, A. & P. Keating 48050 (7); 59761 (7). Gentry, A. & M. Mejía 50705 (21). Gentry, A. & P. Nuñez 54196 (28). Gentry, A. et al. 30911 (7); 48711 (6); 48799 (7); 48804 (7); 61196 (7); 61198 (7); 61200 (7); 61236 (7); 61255 (7); 61256 (7); 61259 (7); 61260 (7); 61265 (7); 71555 (7); 74662 (7). Germain, Ph. s.n. (5). Glaziou, M. A. 19790 (22); 19793 (22); 20444 (22). Goldblatt, P. 1231 (5). Goldman, E. A. 1045 (23). Gómez L. J. 9800 (27); 11772 (6). Gómez, L. D. et al. 23216 (1); 23227 (1). Gómez P., A. 795 (17). Gonzáles, A. 173 (21). Gonzáles, A. & F. Ortega 1363 (21). Gonzáles, J. 790 (7); 800 (28). Grández, C. & A. Kovoov 2883 (7). Grayum, M. et al. 8263 (1); 9702 (7). Gregory, L. E. 134 (21). Guillermo R., J. & D. Cárdenas L. 933 (21). Guindon, C. & D. Brenes 9 (6); 10 (6); 14 (6); 35 (6); 36 (13); 40 (27); 43 (6); 56 (13). Gutierrez B., C. 3711 (17). Guzmán & Santana 1616 (16).
- Haber, W. A. 266 (6); 458 (1); 463 (7); 494 (7); 1424 (6); 2800 (6); 9121 (INB, MO) (1); 9838 (INB, MO) (7). Haber, W. A. & E. Bello C. 1962 (7); 3212 (7); 3477 (7); 4301 (6); 4322 (6); 6371 (7); 6531 (7); 6556 (7); 6559 (7); 6665 (7); 6967 (13); 7081 (7); 7216 (6); 8282 (6); 8264 (6); 8434 (6). Haber, W. A. ex E. Bello C. 4118 (6); 4974 (6). Haber, W. A. ex E. Bello C. & L. Lierheimer 5012 (6). Haber, W. A. & J. Bradford 11538 (6). Haber, W. A. & E. Cruz 7514 (7); 7693 (7); 7721 (7). Haber, W. A. & W. Zuchowski 8502 (1); 8746 (7); 9846 (1); 10749 (6); 11837 (7). Haber, W. A. et al. 8511 (6); 11070 (13); 11092 (27). von Hagen, C. & W. von Hagen 1257 (23). Hahn, L. 1368 (21); 1511 (21); s.n. (21). Hahn, M. s.n. (23). Hammel, B. 6268 (27); 11049 (1); 11766 (7). Hammel, B. & R. Aguilar 18412 (1); 18575 (1). Hammel, B. & E. Chavarría 17539 (7). Hammel, B. & J. Trainer 14992 (1); 17042 (6). Hammel, B. et al. 17502 (13); 18116 (7); 18504 (1); 18716 (1). Harris, W. 5286 (21); 5326 (21); 5575 (21); 5843 (21); 9447 (21). Harris, W. & N. L. Britton 10594 (21). Hartshorn, G. S. 1127 (20); 1465 (7); 2166 (28). Henkel, T. W. 650 (8). Hernández A., C. 174 (2). Hernández G., H. 2663 (12). Herrera, G. 1396 (7); 1559 (6); 1593 (6); 2012 (7); 2381 (7); 3555 (6); 3934 (1); 4643 (MO) (28); 4658 (28); 4992 (7); 5861 (21); 6321 (7); 6605 (7); 8534 (7). Herrera, G. & C. Fallas 4180 (28). Herrera, G. et al. 6678 (1). Hirsch s.n. (P2220?) (7). Hodge, W. H. & B. T. Hodge 1958 (21). Holdridge, L. R. 1053 (21); 6209 (28); 6217 (28); 6595 (20). Holst, B. K. 4435 (12). Holst, B. K. et al. 5236 (17). Howard, R. A. 5695 (21).
- Ibarra M., G. et al. 2292 (12). Ingram, S. & K. Ferrell I. 1666 (7).
- Jack, J. G. 6806 (21); 7016 (21). Játiva, C. 316 (7). Játiva, C. & C. Epling 1096 (7). Jelskii, C. de 187 (28). Jenman 2439 (8); 2515 (8); 5320 (8). Jiménez, Q. et al. 1428 (7). Jiménez S., H. 1816 (28). Jiménez, J. de 3842 (21). Johnson, H. 170 (2). Josse, C. 714 (1). Josse, C. et al. 843 (1). Judd, W. S. 3983 (21).
- Kelly, D. L. 10540 (14). Kenoyer, L. A. 980 (17). Kernan, C. 1269 (1). Kostermans, A. s.n. (7). Krukoff, B. A. 10784 (28); 11235 (28); 11286 (28). Kuhlmann, J. G. 292 (10). Kuhlmann, M. 3885 (9).
- Lao M., R. 66 (28). Lao, E. A. 395 (20). Lasser, F. 2052 (7). Lau, P. 5 (28); 16 (28). Laughlin, R. M. 211 (23). Lawrance, A. E. 353 (28). Lawton, R. O. 1265 (7). Lehman, F. C. 6647 (28); 7226 (28). Leiva G., S. & P. Lezama A. 937 (7). Lems, K. 5164 (21). León, F. et al. 6612 (21); 10451 (21). León, F. & M. Roca 7975 (21). Liebman, M. 711 (= 16) (17); 713 (= 17) (17). Lima, H. C. de et al. 2177 (4); 3707 (22). Liogier, A. H. 11658 (21); 12016 (21); 12616 (21); 14544 (21); 15400 (21). Liogier, A. H. & P. Liogier 19452 (21); 20048 (21); 25140 (21). Little, Jr., E. L. 330 (28); 6293 (7); 6294 (21); 6657 (28); 13594 (21). Loiselle, B. A. 384 (7). Lorea H., F. 5497 (23); 5498 (23). Lorea H., F. & G. Carnevali 5562 (7); 5563 (7). Lorea H., F. & L. Lozada 5533 (17); 5535 (17); 5540 (3); 5553 (17). Lorence, D. H. & R. Cedillo T. 4078 (19). Lorence, D. H. et al. 3871 (17); 4376 (19). Lozano, G. 227 (3). Luna, I. & S. Ocegueda 323 (17); 523 (17). Luna, A. 650 (21). Lundell, C. L. 12232 (17); 19280 (12). Lundell, C. L. & R. Cedillo T. 7165 (17).
- Madrinan, S. & H. Cuadros 652 (28). Marcano-Berti, L. 387 (8); 404 (8); 441 (8); 453 (8); 522 (8); 647 (8); 820 (7). Marcano-Berti, L. & I. Peña 487–979 (7). Marcano-Berti, L. & A. Torres-Lezama 215 (28). Martín, S. 849 (1). Martinelli, G. et al. 12889 (22). Martínez S., E. M. et al. 19456 (19); 22611 (23). Matthews 1433 (14). Maya J., S. 1296 (23); 1697 (23); 2824 (23); 3111 (23); 3349 (23); 4192 (12). McPherson, G. 8973 (7); 12122 (1); 15040 (21); 15312 (6); 15961 (6). McPherson, G. & J. Aranda 10125 (7). McPherson, G. et al. 13370 (7). Meier, W. 1360 (28). Mejía, M. 77 (21). Mejía, M. & J. Pimentel 18334 (21). Mejía, M. & T. Zanoni 12324 (21). Mejía, M. et al. 510 (21); 31389 (21); 35524 (21). Méndez, P. et al. 390 (7). Méndez G., A. & A. Shilom T. 7686 (17). Miers, J. s.n. (2 Feb. 1838) (4). Miers, J. s.n. (date not indicated) (18). Millán, L. A. 21 (7). Miranda, F. 3227 (17); 6003 (23); 6872 (23). Molina R., A. 22952 (23); 31575 (23). Moore, Jr., H. E. & C. W. Wood, Jr. 3957 (17). Mora, A. 36 (6). Morales, C. O. 381 (1). Morales, J. F. 1952 (20);



- 5641 (6). Morega, C. 337 (1). Moreno, P. P. 21657 (23). Mori, S. et al. 8159 (8); 23377 (11). Morton, C. Y. 9563 (21). Müller 1460 (17). Murphy, H. 423 (28).  
Nash, G. V. & N. Taylor 1035 (21). Neill, D. et al. 7477 (28); 9066 (21); 9782 (28). Nr 547 (18). Nunes, G. M. 313 (25); 323 (10). Núñez, A. 1159 (3).  
Ocegueda, S. & O. Alcantara 363 (17). Ocegueda, S. & I. Luna 210 (17). Ortega U., A. 138 (28).  
Palacios, W. 4655 (21); 4804 (28); 4842 (7); 10794 (21); 12725 (7). Palacios, W. & C. Iguago 4852 (7). Palacios, W. & D. Rubio 7304 (7); 7350 (7). Palacios, W. & M. Tirado 13147 (14). Palacios, W. et al. 9554 (28); 13568 (1); 13616 (1). Pennington, T. D. & L. J. Poveda 11416 (13). Pennington, T. D. & J. Sarukhán K. 9265 (2); 9645 (2). Peralta, R. s.n. (28). Persaud, A. C. 70 (8). Personal do Horto Florestal 85 (10); 87 (4); 102161 (10). Philippi, R. A. 906 (5); 964 (18); s.n. (18). Philipson, W. R. et al. 2094 (28); 2163 (28). Pimentel, J. 242 (21). Pittier, H. 1286 (28); 2040 (20); 3084 (20). Plée 204 (21). Poortmann s.n. (7). Popenoe, W. 754 (2); 884 (2); 1304 (1); s.n. (1189?) (2). Póveda, L. J. 449 (1); 1068 (CR, F) (7). Póveda, L. J. & J. A. Soeng 1524 (1). Póveda, L. J. et al. 3019 (7). Proctor, G. R. 33607 (21); 33791 (21); 37316 (21); 39101 (21). Purpus, C. A. 8745 (17).  
Quelal, C. & G. Tipaz 78 (7); 124 (7). Quelal, C. et al. 459 (28).  
R. to. de V.? s.n. (18). Raimondi 6248 (28). Ramírez 4104 (28). Remy 108 (18). Richard, L. C. s.n. (21). Rico A., L. & R. López 800 (23). Riedel 1585 (9). Rincón G., A. 419 (19); 433 (19). Rivera, G. 174 (20); 612 (6). Rivera, N. 324 (28). Rodríguez, G. & Q. Jiménez 116 (7). Rodríguez, L. C. 374 (23). Rojas, E. 28 (7). Rubio, H. 353 (17); 362 (17); 530 (17); 629 (17); 935 (17); 1695 (17); 2209 (17). Ryan, J. s.n. (21). Rzedowski, J. 10975 (17); 12383 (17); 23419 (17); 29973 (17); 46423 (17); 46588 (17).  
Sagastegui A., A. et al. 12408 (7). Samaniego V., A. & F. A. Vivar C. 79 (7). Sandwith, N. Y. 288 (8). Schipp, W. A. 1262 (12). Schlegel, F. 5927 (18); 6247 (18). Schomburgk, M. 1009 (8); 1730 (K) (8). Seidel 5761 (28). Servín, B. 27 (17); 339 (17); 484 (17); 900 (17); 1329 (17). Shafer, J. A. 588 (21). Shauk 13955 (F) (7). Silverstone-Sopkin, P. & N. Paz 7493 (7). Sintenis, P. 2678 (21); 4137 (21); 4398 (21); 4700 (21); 5317 (21); 6523 (21). Solheim, S. L. & M. Chazaro B. 1718 (17). Smith, A. 2717 (6); 4168 (20); H592 (7); NY675 (20); P2418 (7). Smith, D. N. & A. Pretel 7615 (28); 8004 (14). Smith, H. 2104 (1). Soto N., J. C. & E. M. Martínez S. 5122 (17). Sousa, M. et al. 7871 (19). Standley, P. C. 10484 (23); 10787 (23); 10857 (23); 24627 (2); 60223 (F) (2). Standley, P. C. & R. Torres R. 51271 (7); 51285 (7). Standley, P. C. & J. Valerio 51280 (7). Stern, W. L. & K. L. Chambers 173 (21). Stein, B. A. 3635 (14). Stein, B. A. & C. Todzia 2231 (28). Stevens, W. D. et al. 20891 (21). Steyermark, J. A. 44494 (24); 54404 (14); 56933 (28); 89161 (8); 89880 (7); 104700 (28). Steyermark, J. A. & V. C. Espinoza 106806 (28). Steyermark, J. A. et al. 98386 (14); 98480 (14); 100700 (14). Stork, H. E. 1713 (F) (7). Sucre, D. et al. 10058 (10). Swartz s.n. (21). Sytsma, K. & W. D. Stevens 2148 (20).  
Tanner, E. & B. Kapos 709 (14). Taylor, C. M. & M. Nee 260 (17). Taylor, C. M. & M. Muñoz S. 10883 (18). Téllez 6551 (23). Tello 590 (7). Tenorio L., P. et al. 8669 (17); 9000 (17); 12612 (17); 12726 (17); 14260 (17). Terrán, L. R. 1065 (14). Thomas, H. 412 (12); 420 (12); 584 (20). Thomsen, K. 58818 (7). Thorne, R. F. 38072 (18). Thorne, R. F. & G. R. Proctor 48212 (21). Tipaz, G. & C. Quelal 141 (7); 652 (1). Tipaz, G. et al. 792 (28). Tirado 1350 (7). Tonduz, A. 11713 (7). Toriz A., G. et al. 297 (17); 324 (17). Toro, R. A. 895 (28). Torres C., R. et al. 2947 (19). Tutin, T. G. 114 (8).  
Utley, J. & K. Utley 4653 (7).  
Vargas, W. 754 (28); 1349 (1). Veillon, J-P. II/12 (21). Velásquez, P. & O. Marulanda 7754 (14). Ventura A., F. 11312 (17). Villalobos, R. 1 (7). Villalobos C., G. & E. Guerrero 138 (2); 139 (2); 244 (2).  
Wendt, T. & L. Rico A. 4338 (23). Wendt, T. et al. 5151 (12); 5350 (12); 5406 (12); 6733 (12); 6886 (12); TP-217 (12); TP-217-B (12). Werff, H. van der 12256 (1); 12951 (11). Werff, H. van der & W. Palacios 10574 (7); 10584 (28). Werff, H. van der et al. 7575 (28); 8224 (14); 8329 (28); 8333 (28); 8766 (28); 8786 (7); 12163 (28); 12168 (7); 12289 (1); 12406 (28); 13368 (7); 13377 (28); 13389 (7); 14015 (6); 14029 (7); 15491 (7); 15585 (7); 15761 (28); 15831 (28). West, J. 5195 (18). Weston, A. S. 4868 (20). Wheelwright, N. T. 52 (6); 55 (6); 70 (6); 126B (7); 188/A (7); 206 (1); 219 (7). White, C. E. 1051 (28). Williams, L. 7077 (28); 10253 (7); 11073 (7). Williams, L. O. & A. Molina R. 42575 (23). Wright, C. 485 (21); 486 (21); 1402 (21); 1403 (21); 1414 (21).  
Yasuda, S. & R. Aguilar 1315 (21); 1316 (1). Yasuda, S. et al. 1300 (20); 1301 (20); 1307 (27); 1308 (1); 1309 (7); 1310 (6); 1311 (6); 1312 (13); 1313 (27); 1314 (6).  
Zamora, N. 1321 (6). Zamora, N. et al. 1215 (1); 1817 (21); 1819 (28). Zanoni, T. & R. García 36285 (21). Zanoni, T. & M. Mejía 12311 (21). Zanoni, T. & J. Pimentel 36009 (21). Zanoni, T. et al. 12569 (21); 16686 (21); 19410 (21); 24313 (21); 29152 (21); 32890 (21); 34216 (21); 36238 (21); 40676 (21); 43103 (21); 44246 (21); 44284 (21). Zaruma, J. & A. Arguello 485 (7). Zetek 5149 (28). Zöllner, O. 11607 (18); 18999 (18).